Systematic Zoology

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Systematic Zoology

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Dispersal of Cavernicolous Beetles[1]

CARL H. KREKELER

IN North American caves there live beetles of several families, such as the Pselaphidae, Staphylinidae, Catopidae, and Carabidae. In the subfamily Trechinae of the last mentioned family five genera are known (*Pseudanophthalmus, Neaphaenops, Ameroduvalius, Darlingtonea,* and *Nelsonites*) which live in caves and are highly modified. Specifically they are generally eyeless, wingless, and depigmented, and possess attenuate legs, antennae, and setae. Beetles of these genera, commonly referred to as anophthalmids, are considered true cave forms. One genus, *Pseudanophthalmus,* is by far the most abundant and widespread. Largely on the basis of excellent work by Valentine and Jeannel in the past few decades, this genus is now known to consist of almost a hundred described forms from six states. This report will be based on forms of this genus.

There is no record of *Pseudanophthalmus* ever having been taken outside a cave. Thus it might seem strange at first glance that information relative to insect dispersal might come from a study of this genus. Yet these forms are of great interest, and especially with respect to dispersal, just because they are restricted to caves. Populations isolated in caves have in many cases accumulated distinctive characteristics, particularly in aedeagal structures, on the basis of which they are describable as distinct forms. But, in addition, the forms within a given area are generally found to be more closely related to one another than to forms from a distant area. This would seem to indicate that one or several things have happened.

At one extreme it could be that trechines without anophthalmid characteristics, living at one time in the present cave area and to a certain extent at least outside caves, became divided into a number of geographic forms. For some reason they became essentially restricted to caves, and populations in isolation have accumulated differences on the basis of which they may be described as distinctive forms but yet belonging to common groups. Since these trechines were not "anophthalmid" at the time they became restricted to caves, a great number of cases of parallel regression would have had to occur. This might seem quite improbable, but the fact is that Jeannel (1928) has described a number of examples in Europe in which there appears to be a gradation between the epigaean winged, pigmented, and eyed forms and their hypogaean relatives which lack wings, heavy pigment, and eyes. At this extreme, dispersal would be considered as essentially above ground and largely in the past.

At the other extreme, it could be that anophthalmid type trechines have very rarely arisen from epigaean forms. From one or a few basic stocks have arisen the many known forms, as anophthalmids have dispersed widely from one or a few sites of origin. Such dispersal might be thought of as occurring regularly in subterranean passages, though overland dispersal need not be considered impossible.

What has actually occurred probably lies somewhere between these two extremes. In any event, however, dispersal of some sort occurred, and such dispersal has resulted in present distribution patterns. What information we have concerning dispersal of cavernicolous beetles comes from a careful examination of these distribution patterns in relation to physiographic and geologic data and what is thought to be

[1] Presented at a symposium on Mechanisms of Species Dispersal sponsored by the North Central Branch of the Entomological Society of America at Columbus, Ohio, March 26, 1959.

the range of tolerance and the behavioral patterns of anophthalmids. The fact is that tolerances and behavior of anophthalmids have not been systematically studied. It is generally presumed, however, that inasmuch as these beetles are regularly found in moist and cool environments they are intolerant of dry and warm environments. Experiences in attempting to transport and maintain them tend to confirm this assumption. A variety of behavior patterns relative to movement have been observed in the field. At one extreme, some forms of anophthalmids seem to move about regularly on the surface of mud banks, rocks, and gravel. At the other extreme, other forms seem more regularly to lie quietly beneath rocks and in crevices. What these observations mean for dispersal is difficult to say.

It is on this general basis that it is possible to present opinions on the dispersal of the anophthalmids, particularly *Pseudanophthalmus.*

Illustrative Example

It may be well to begin with the consideration of an example that illustrates many of the problems encountered. Forms of the *grandis* group of *Pseudanophthalmus* are found, as indicated in Figure 1, in caves of the Greenbrier River valley in southeastern West Virginia. This region is a portion of the Appalachian Plateau and the caves are formed in the Greenbrier series of limestones which, in general, lie relatively horizontally in this area. This valley is pocked with sink holes of all sizes and forms, and a number of streams flow into sink holes and disappear underground. The picture, in short, is that of a relatively flat valley with bedrock of limestone honeycombed with a network of underground passages. The larger passages which have been exposed by surface erosion comprise what are called caves, which in this specific region number over a hundred. Many of these caves are undoubtedly interconnected by underground passageways not large enough to be traversed by man but certainly of sufficient size to provide for movement of anophthalmids.

Populations which cannot be distinguished from one another and which have been designated *P. grandis grandis* by Valentine (1932) have been taken from a number of caves to the north and northeast of Lewisburg (Valentine, 1931, 1932; Jeannel, 1949). Apparently the streams of several of these caves, Coffman Cave and the Higginbotham caves, are part of a common drainage net (Davies, 1949), and it is quite possible that the other caves connect with the same network. The exact underground pattern of streams within the caves is not known.

Populations not distinguishable from one another, yet apparently distinct from *P. grandis grandis* and designated *P. grandis elevatus* by Valentine (1932), have been taken from caves to the south and southwest of Lewisburg. Two of these, Foxhole Cave and Organ Cave, are known to be sections of a single cave system (Davies, 1949). One may wonder, however, whether underground passages can connect this system to General Davis Cave which lies on the opposite side of the Greenbrier River and/or whether the form from General Davis Cave is indeed the same as that from Organ Cave.

In the *grandis* group are included several other forms. One of these, *P. henroti,* is known only from a single male taken from Arbuckle Cave in association with *grandis grandis.* The other forms, as shown in Figure 1, are found in caves some distance away from the systems in which the forms of *P. grandis* are known. A complex of synclinal and anticlinal mountains separates the locations of *P. hypertrichosis* and *P. grandis,* hence it is improbable that underground channels connect these caves. It is not known whether the Greenville caves containing *orthosulcatus* are or are not connected by underground channels with the caves toward Lewisburg. Even if they were,

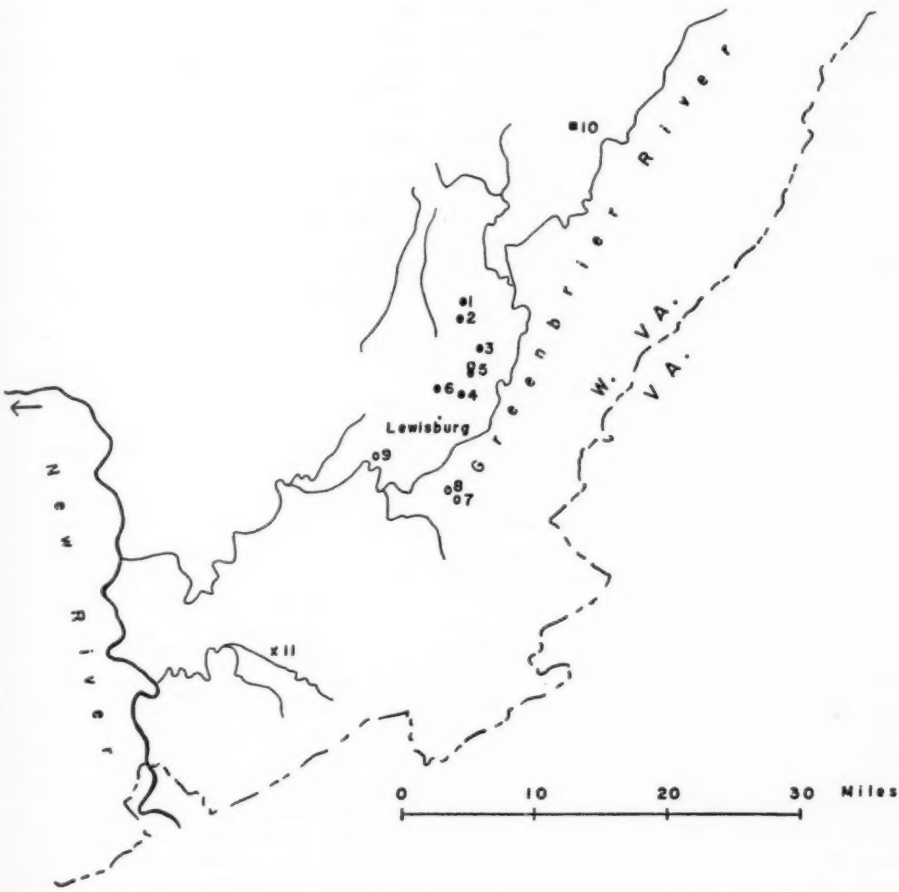

FIG. 1. Distribution of forms of *grandis* group of *Pseudanophthalmus* in southeastern West Virginia.

● *P. grandis grandis:* 1, Higginbotham Caves; 2, Coffman Cave; 3, McClung Cave; 4, Brandt Cave; 5, Arbuckle Cave; 6, Grape Vine Cave.
○ *P. grandis elevatus:* 7, Organ Cave; 8, Fox Hole Cave; 9, General Davis Cave.
□ *P. henroti:* 5, Arbuckle Cave.
■ *P. hypertrichosis:* 10, Marthas Cave.
× *P. orthosulcatus:* 11, Greenville Cave.

the connections would be over a long distance and must therefore be considered extremely tenuous. On the basis of a preliminary examination of the aedeagus of a male specimen taken from this cave system by the author it is not clear whether Jeannel (1949) is justified in his designation of this form, known then from a single female, as *P. orthosulcatus*. Valentine (1932) designated it *P. grandis orthosulcatus*.

It should be pointed out before going further that inhabiting many of the same caves as forms of group *grandis* are forms

of *Pseudanophthalmus* belonging to two additional groups. Moreover, a number of additional specimens representing all three groups have been collected by the author and Barr (personal communication) in this general area. The pattern of the forms already described, and of the undescribed materials studied so far only in a preliminary fashion, does not seem to differ basically from that described above.

One might summarize this pattern in this way. In an area where caverniferous strata are relatively level, subsurface drainage assumes great significance and underground channels are extensively developed. Forms such as anophthalmids may have dispersed and may continue to move regularly through such channels, and anophthalmids taken from caves connected by such channels may be expected to exchange genes regularly and exist as indistinguishable populations. In cases where connections are more extended and tenuous, dispersal may have been and may continue to be accomplished, though less readily. Gene exchange may be limited to such an extent that subpopulations may acquire distinctive features on the basis of which, in conformity with practice usual in taxonomy, they may be described as subspecies. In cases where there are obvious physiographic or stratigraphic barriers to dispersal, and perhaps even where possible underground connections are extremely long and tenuous, it is clear that dispersal has occurred at some time in the past. But one would consider present movement between caves separated in this manner as highly improbable. Exchange of genes between populations isolated in this manner is essentially non-existent, and such populations seem generally to meet usual taxonomic criteria for designation as distinct species.

Extent of Present Dispersal

Patterns similar to this of the Greenbrier valley, in which in at least a portion of the range the same form is known to inhabit a number of caves, seem to exist in other areas. Barr (1959) describes and discusses such situations in some detail for the Mammoth Cave area and the Red River valley of Tennessee and Kentucky.

In still other areas, however, it seems that each cave, or each individual cave system consisting of a few immediately adjacent caves, contains its own peculiar form of anophthalmid. Again dispersal between such caves has obviously occurred in the past. But it has been rather generally assumed that dispersal between these caves at present is non-existent. Jeannel and Valentine in describing distinctive populations from such caves have described those forms as subspecies which differ from one another quantitatively rather than qualitatively, though the difficulty of distinguishing between quantitative and qualitative differences is in many cases admittedly difficult. The present author (Krekeler, 1958) has described distinctive populations as species, considering it desirable for both practical and theoretical reasons to use Emerson's (1945) criterion of reproductive isolation, whether extrinsically or intrinsically determined, as the criterion for delimitation of species. Going largely on the assumption that dispersal between caves is essentially non-existent, he felt that, practically speaking, the criterion of reproductive isolation could be more readily applied than could morphological criteria. This assumption of rather complete isolation of anophthalmid populations, however, has been sharply questioned by Barr (1959 and in personal communications). Both the preceding and following portions of this report include data on the basis of which we can judge this assumption, and we shall return to the matter later.

Correlation of Distribution with Drainage

The type of distribution pattern which has been considered the usual one for anophthalmids is that in which forms of a group or of closely related groups are

found to occupy a single drainage basin or a series of interconnected drainage basins. One of the best examples of such correlation is that of the *engelhardti* group in the Tennessee River basin as described by Valentine (1931, 1932, 1937, 1945, 1948) and outlined in Figure 2.

Nine forms may be considered subspecies of *P. lodingi*. These, as indicated in Figure 2, are found in caves near the Tennessee River or its tributaries along the course of the Tennessee immediately prior to and along its course through Alabama. Those subspecies south of the Tennessee River (*distinguens, fluviatilis, meridionalis,* and *fulleri*) are quite clearly more closely related to one another than to the other forms. With respect to the first three, Valentine (1948, p. 13) points out that they are found in caves along minor tributaries heading north to the main river, and suggests that "a very perfect racial cline can doubtless be established between *meridionalis* at the bend of

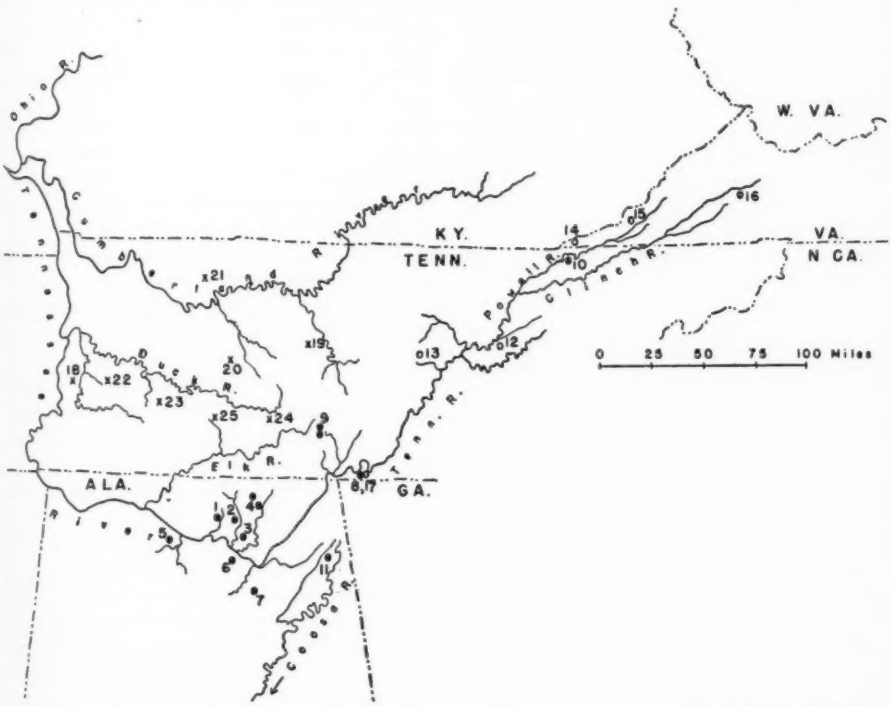

FIG. 2. Distribution of forms of *engelhardti* group and possibly related forms of *Pseudanophthalmus*.

Data from Valentine (1932, 1937, 1945, 1948) and Jeannel (1949).

● forms of group *engelhardti:* 1, *P. lodingi lodingi;* 2, *P. l. profundus;* 3, *P. l. aquaticus;* 4, *P. l. aladdini;* 5, *P. l. distinguens;* 6, *P. l. fluviatilis;* 7, *P. l. meridionalis;* 8, *P. l. fulleri;* 9, *P. l. humeralis* (also *P. intermedius*); 10, *P. engelhardti* and *P. rotundatus;* 11, *P. alabamae.*

○ forms possibly related to group *engelhardti:* 12, *P. tenesensis;* 13, *P. jonesi;* 14, *P. hirsutus hirsutus;* 15, *P. h. delicatus;* 16, *P. hubrichti;* 17, *P. digitus.*

Data from Barr (1959).

× forms of group *engelhardti:* 18, *P. hesperus;* 19, *P. tiresias tiresias;* 20, *P. t. acherontis;* 21, *P. t. insularis;* 22, *P. t. occidentalis;* 23, *P. t. bendermani;* 24, *P. t. tullahoma;* 25, *P. t. catherinae.*

the river and *distinguens*, 45 miles to the northwest, . . . when the caves of this interesting region yield additional material."

The forms north of the Tennessee in Alabama (*lodingi s. str., profundus, aquaticus,* and *aladdini*) are similarly most closely related. In this case Valentine makes the point that *profundus* is more closely related to *aquaticus,* whose type locality is 10 miles distant from its own but in the same Flint River drainage, than it is to *lodingi* whose type locality is but five miles distant but in the Indian Creek drainage. *P. humeralis,* taken from two caves lying adjacent to one another, seems to be closely related to the other forms.

Additional data provide a more complex picture. Along the Powell River, a tributary of the upper reaches of the Tennessee, is found *P. engelhardti.* This form is most closely related to *humeralis,* its aedeagus being somewhat intermediate in type between that of *lodingi* and *humeralis.* If it were not for the great distance separating this form from the closest *lodingi* form, 200 miles, Valentine would consider it a subspecies of *lodingi.* Inhabiting the same cave as *engelhardti* is *P. rotundatus.* This form, while unquestionably a distinct species, belongs to the same general group. The facts concerning these two forms would, of course, tend to fit into the pattern of relation of anophthalmid distribution to drainage pattern though the great distance separating the caves is anomolous. The other forms shown in Figure 2 along the tributaries of the upper reaches of the Tennessee would also fit into this pattern. Not too much weight can be placed on these forms, however. The relationship of *tenesensis* and *jonesi* to each other and to the *engelhardti* group is not clear. Though there has been some question (Valentine, 1948), *P. hubrichti* appears (Barr, personal communication) to be related to the forms described as subspecies of *P. hirsutus;* there is still the question (Valentine, 1932) whether *P. digitus,* known only from a female inhabiting the same cave as *fulleri,* is similarly related; Jeannel (1949) assigns these forms to the *hirsutus* group with reservations.

The two remaining records of Valentine listed in Figure 2 are definitely exceptions to the pattern of finding related anophthalmids in a given drainage basin. *P. intermedius* is found in Crystal and Wonder Caves whose streams likely join the waters of the Elk River which flows to the Tennessee. Other forms related to *intermedius* come from caves of the Cumberland drainage to the north. Valentine (1945) comments that it is interesting that these two caves lie near the divide between these two watersheds. *P. alabamae* is found in a cave at the foot of Lookout Mountain in the Coosa River drainage which extends south to the Gulf of Mexico. This species is definitely related to *engelhardti* and probably should be included in that group as Jeannel (1949) does, though Valentine (1932) does not. In commenting on the presence of this form in a drainage basin adjacent to that of the Tennessee, Valentine (1932) notes that Lookout Mountain is thought to be cavernous throughout its extent and seems to postulate that anophthalmids have moved between the two basins via such channels.

Another area in which quite striking correlations of drainage and anophthalmid relationships are described by Valentine is along the Potomac River and its tributaries in Virginia. In general, Valentine and Jeannel in reviewing the taxonomy of North American anophthalmids imply an acceptance of correlation of relationship and drainage by their emphasis on the drainage basin in which a given group is found, even though exceptions are duly noted. Barr in his recent (1959) paper presents still further examples of relatively sharp breaks in fauna corresponding to drainage divides. Such correlation undoubtedly exists and must be accounted for. But it seems that any explanations

that are suggested should account also for the exceptions. This would seem to be particularly important since some of the more recent reports (Krekeler, 1958; Barr, 1959) and preliminary studies of the materials with which the author is currently working have disclosed a number of cases in which striking exceptions to the pattern are found.

Possible Types of Dispersal

What type of dispersal may be proposed to account for this general pattern as well as the exceptional cases? If dispersal is related to stream courses, is its direction headward, downstream, or both? Is it subterranean or at the surface? When divides are crossed is it because of stream phenomena such as piracy, either surface or underground, or do anophthalmids have the ability to move overland from one basin to the other? To what extent is dispersal not necessarily related to stream courses? Our best course in attempting to arrive at answers to these questions seems to be to list the possibilities, relate them to the tolerances and behavior of anophthalmids as far as they are known, and, as we consider patterns of distribution, attempt to arrive at a most likely mode of dispersal.

We follow this course first of all in discussing the direction of movement, for there is no clear evidence from the evolution of the anophthalmids themselves as to direction. It would seem quite possible for anophthalmids to be washed downstream. Anophthalmids are found regularly near the water of cave streams which may rise rapidly and wash with considerable force through a cave. Anophthalmids seem quite tolerant of being covered with and carried along by water, and there is no reason to believe that such accidental dispersal is not possible. But anophthalmids must somehow also move headward, for as seen in Figure 2 the caves from which very closely related forms are taken lie, in a number of cases, upstream along separate tributaries of a major stream. One would hardly suggest that such movement is through the water itself. There would, rather, seem to be two major possible types of movement within stream valleys which might account for either headward or downstream movement.

One possibility is that movement is along the banks of streams where conditions of moisture and temperature are probably more likely than elsewhere to be within the range of tolerance of cavernicolous forms. Or it may be that stream valleys in general, not necessarily the region immediately adjacent to the stream, are favorable for movement at given times and/or under given climatic conditions. At least stream valleys would not seem to constitute major barriers to dispersal as readily as high and rugged divides would seem to. Though we may refer to this type of dispersal as overland movement it need not be strictly at the surface; it may well be beneath litter, along crevices, etc.

Another possibility is that anophthalmids move parallel to streams along subterranean channels subparallel to surface streams. Barr (1959) discusses this possibility in some detail, pointing out that for various reasons it is often, though not always, true that subterranean drainage channels tend to parallel surface streams. Such channels when no longer completely filled with water would allow for movement of anophthalmids.

According to either of the two above possibilities, while a general pattern of correlation of related forms of anophthalmids with related drainages would be expected, exceptions could be accounted for. In the case of surface movement one would simply have to postulate that the pattern of divides has changed as a result of physiographic processes such as stream piracy and/or that low divides do not constitute major barriers to dispersal. In the case of underground movement one would simply have to postulate that underground channels do not always parallel surface drainage and/or that underground

divides do not necessarily correspond to surface divides. The question now is whether one of the two possibilities is more likely than the other to help account for the pattern and its exceptions. It may be that an examination of exceptional cases will be of most value in helping us find an answer to this question. Of the numerous exceptions which have now been brought to light the most illuminating seem to be as follows.

Evidence for Underground Dispersal

Barr (1959) has recently described a number of new forms which are probably to be included in the *engelhardti* group. Of these forms, identified by special symbol in Figure 2, some may be considered to fit into the pattern of distribution along the Tennessee River and its tributaries such as Elk River, Duck River, and Buffalo River. Duck River and Buffalo River, however, are quite some distance downstream from those forms described by Valentine, and stream distances between these localities are certainly long. Definitely exceptional is the distribution of forms in caves along the Cumberland River and its tributaries such as Caney Fork and Stones River. Seven of these forms, spread widely over this area in different drainages, are so similar morphologically that they are described as weakly defined subspecies of *tiresias*.

In discussing this pattern, among others, Barr (1959) emphasizes the possibilities of underground movement. He points out that the range of *tiresias* corresponds approximately to the Central Basin of Tennessee, that the rock strata of this physiographic unit are relatively flat-lying, and that caverns are known from most of the limestone formations in the basin. Although he does not attempt to describe in any detail how an underground system of interconnected channels would account for the distribution pattern of *tiresias*, he seems to suggest that dispersal has been along a subterranean system not corresponding in many respects to surface drainage, with subterranean divides specifically not corresponding with surface divides. In a sense this represents an extension over a broad area of the picture presented above for the Greenbrier valley. In an extended system such as the Central Basin, however, one might well expect that distances alone would be sufficiently great to effect partial isolation of populations.

It seems that one must recognize dispersal by way of underground channels as a distinct possibility. In most cases it may be impossible to demonstrate the extent of underground channels because of their very nature. In accepting such underground dispersal possibilities, however, care must be taken not to postulate underground connections indiscriminately. Moreover one must not assume regular movement at present between caves between which dispersal has occurred in the past; and one must keep in mind that an improbable dispersal may account for the colonization of a cave but that a more regular or probable movement between caves is required for exchange of genes. Limits to the extent of underground connections can probably be established in some cases on the basis of information relative to the dip of the strata, levels of the caves, depth of valley cutting between caves, and other such data. As work with the anophthalmids proceeds we shall probably find such data assuming more and more significance.

Evidence for Overland Dispersal

Another exceptional distribution pattern is exhibited by forms of group *inexpectatus*. One species, *P. inexpectatus*, has been described (Barr, 1959), and others will be in the near future (Krekeler, in preparation). As shown in Figure 3, some of the forms are in the Kentucky River drainage basin, others in the Salt River-Rolling Fork basin, and still others in the Green River basin. This distribution is quite apparently not correlated with present stream valleys.

What is of special significance in this group is that the caves concerned are found in limestone strata of two distinct geological periods between which lie strata not likely to contain caves. Some of the caves are found in the Blue Grass physiographic unit, a region characterized by outcropping of Ordovician limestone but including some Silurian and Devonian limestones. This Blue Grass region in Kentucky is fringed on the west, south, and east with outcropping of Devonian and Lower Mississippian strata which form a Knobs region indicated by stippling in Figure 3. Other caves from which species of this group have been taken are in the Mississippian Plateau, a region of Middle and Upper Mississippian limestones. A structure section showing the dip and types of the strata in this general area is included in Figure 3. It is especially important that among the geological strata of the Knobs region, in addition to limestone and dolomite, are a succession of black shales of Devonian age and gray to green clay-shales and siltstones of the Lower Mississippian.

Because of the dip of the strata in the area in question and because caves, and certainly extensive cavern systems, are not at all likely to develop in shales, it would seem quite certain that there are no underground connections between the two groups of caves on either side of the Knobs region. Thus all the evidence points to a dispersal of the forms of group *in-*

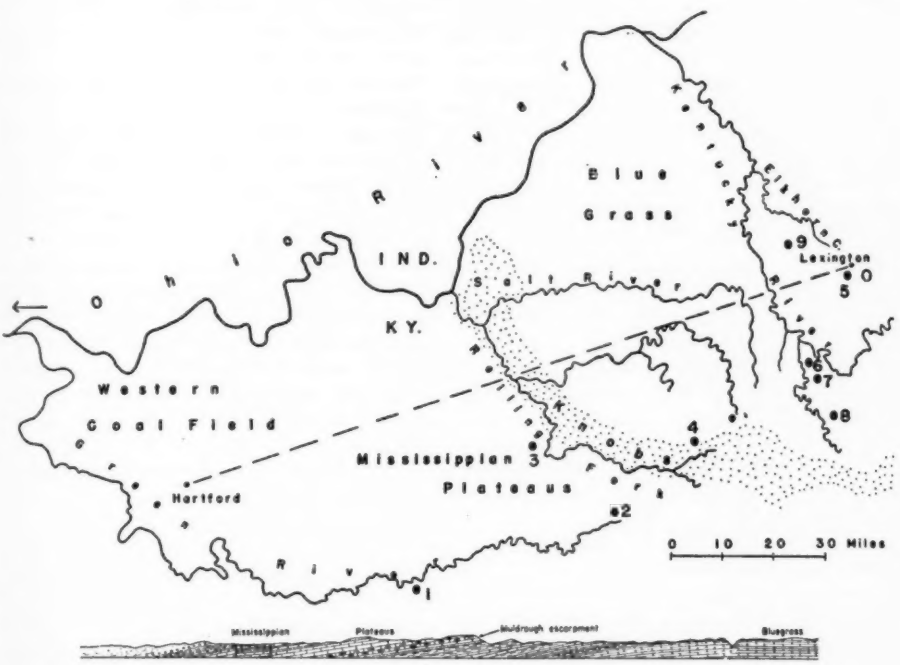

FIG. 3. Distribution of forms of the group *inexpectatus* of *Pseudanophthalmus* in central Kentucky in relation to physiography and geology. 1, White Cave; 2, Phillips Cave; 3, Eli Reed Cave; 4, Tatum Cave; 5, Picadome Cave; 6, Ison Cave; 7, Arnold Cave; 8, Robinson Cave; 9, Swope Cave.

Below: structure section from near Hartford northeast to near Lexington along broken line in figure; vertical exaggeration times 20 (from Geologic Map of Kentucky, 1954).

expectatus overland across the Knobs region from one drainage basin to another.

Effect of Glaciation on Dispersal

One further point that we must take into account when considering drainage basins as channels of dispersion is that changes in drainage patterns were brought about by glacial stream diversions. In areas cited heretofore, unglaciated regions some distance from glacial fronts, few such changes are likely to have occurred. But in regions nearer the ice margins, as in Indiana and northern Kentucky, many changes in drainage lines took place as consequences of glaciation.

As far as the distribution pattern of North American anophthalmids is concerned, one of the most significant changes in drainage caused by glaciation was the disruption of a preglacial river named the Teays. The Teays and its tributaries drained much of the area in which anophthalmids are known to exist. It headed in the highlands of the Carolinas, then followed a course now occupied in part by the Kanawha, Ohio, and Scioto Rivers to near Chillicothe, Ohio, from where it continued in a northwesterly direction across Ohio, Indiana, and Illinois to the Mississippi (Tight, 1903; Horberg, 1950; Janssen, 1953; Wayne, 1956). This system was highly modified by glaciation. That part of the stream crossing central Ohio, Indiana, and Illinois was disrupted by glacial activity in the Nebraskan or Kansan Age, probably the latter (Wayne, 1956). The present Ohio River was formed as a channel cut through divides to connect the upper courses of the Teays with the preglacial Ohio, which was a relatively small stream that may have headed in the uplands near Madison, Indiana (Malott, 1922; Fowke, 1925; Wayne, 1952). This picture so far seems to help to account for some minor distributional patterns, and has helped us to establish a minimal date on the isolation of two closely related forms found on either side of the Ohio River (*cf.* Krekeler, 1958). But attempts to arrive at major correlations with preglacial or interglacial drainage so far are quite speculative and certainly are not strikingly positive. Yet such antecedents of modern drainage must be taken into account in the consideration of anophthalmid dispersal. Dispersal in the past, if dispersal is influenced in any way at all by stream patterns, must have been in relation to past patterns in areas where past drainage patterns differed to any significant extent from the present ones.

Conclusions

In attempting to bring these various considerations together, the following points might be made. It would seem that dispersal in anophthalmids may be accomplished along underground channels or overland. In either case present stream divides may be crossed although in a great many cases related forms tend to be distributed within a given drainage basin, either because underground channels tend to parallel surface streams or because conditions for dispersal are most favorable within such a basin.

Which of the two routes of dispersal has been of greatest significance in the past is difficult to determine. In one case, at least, overland dispersal would seem to be required. In another case underground dispersal would seem quite possible. Certainly the two routes are not mutually exclusive.

One cannot rule out the possibility that dispersal between caves occurs today. Having reviewed the evidence, the author has come to the conclusion that, in attempting to arrive at an estimate of the degree of gene exchange between populations, it is probably more difficult to establish that dispersal is not physically possible between caves than it is to apply standard morphological techniques. In many cases it is easier to assess the value of quantitative differences between forms than it is to establish that anophthalmid populations are prevented by extrinsic

factors from exchanging genes. Therefore, reversing a policy followed in his 1958 paper, he concludes that subspecific ranks are probably a necessary and useful tool in the description of anophthalmids.

The problem remains of how to handle forms which, if analyzed on the basis of morphological criteria alone, would be considered subspecies but which, on the basis of known physiographic data, great distances, or impassable barriers, can be said almost certainly to be completely isolated. For example, should *engelhardti* be considered a distinct species rather than a subspecies of *P. lodingi* on the basis of the great distance separating them?

It may be argued, on one hand, that if one were to use morphological criteria exclusively the taxonomic data would be most consistent and valuable. Specifically, in applying such data to an evaluation of the role of isolation in speciation the danger of falling into the error of circular reasoning would be minimized. In this case those forms would be designated subspecies which are judged by morphological criteria as probably exchanging some genes no matter how improbable such exchange would seem at present on the basis of physiographic data. And those forms would be designated species which are judged by morphological criteria as probably not exchanging genes.

It should be pointed out, on the other hand, that there is much merit in the use of reproductive isolation, whether extrinsically or intrinsically determined, as a criterion for the delimitation of species. The author discusses some of the theoretical reasons for this approach in a previous paper (1958). Valentine in considering *engelhardti* a species distinct from *lodingi* and Jeannel in considering *barberi* of Kentucky a species distinct from very closely related forms across the Ohio River in Indiana have essentially followed this procedure. One using these taxonomic data in a discussion of the role of isolation in speciation should be familiar with these practices. In this case those forms would be designated subspecies which are judged by morphological criteria as probably exchanging some genes and for which there is no evidence that it is probable that extrinsic factors prevent exchange of genes. And those forms would be designated species which are judged by morphological criteria as probably not exchanging genes or for which there is evidence that probably extrinsic factors prevent exchange of genes.

It is the author's opinion that both theoretical and practical arguments weigh in favor of the latter alternative. It differs from his previous position in that it assumes the possibility of interconnections between caves unless there is evidence to the contrary rather than assuming the lack of interconnections between caves unless there is evidence to the contrary.

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The Tracheal System as a Systematic Character in Larval Diptera

JOAN M. WHITTEN

MOST insect systematics is based on external morphology, and certainly in the Diptera internal larval anatomy has not been previously studied comparatively. In a series of papers the author (Whitten, 1955, 1956a, 1956b, 1957) has described the tracheal system in certain larval Diptera; the results are interesting from a taxonomic as well as a comparative morphological point of view. The tracheal system has long been considered a system which is readily adapted to different environmental conditions. In the Diptera we find every spiracular condition ranging from the holopneustic Bibionidae with all ten spiracles functional (Fig. 1A), to the Chironomidae and Ceratopogonidae which are apneustic with no functional spiracles. There is also great diversity in internal tracheal form, which might suggest that the tracheal system is an unstable character with an infinite capacity for variation. Comparative morphological results show that there is an underlying pattern present even in the most anomalous systems. These results strongly suggest that the system is not only stable, but can provide a useful taxonomic character in segregates where variations are found.

The origin of the tracheal system in the Diptera is monophyletic, since every example from each of the families studied can be interpreted in terms of a 'basic framework' or pattern (Fig. 1 and Table 1). The constituent tracheae of this pattern are two dorsal and two lateral longitudinal trunks; ten dorsal anastomoses; eight transverse connectives joining the two trunks on each side; two dorsal and two ventral cervical tracheae; a dorsal cervical anastomosis, and a series of ventral ganglionic tracheae, the first three of which form three mid-ventral anastomoses.

The different members of the Diptera can be divided into two categories with regard to their tracheal systems: a) those retaining a full complement of tracheae

and anastomoses, and thus possessing the generalized pattern deduced for the order, and b) those deviating from the basic pattern by reduction of one or more of the tracheal anastomoses or connections. To the first group belong the nematoceran families Anisopidae, Trichoceridae, Bibionidae, Psychodidae, and the Brachycera and Cyclorrhapha. To the second group belong the nematoceran families Tipulidae, Mycetophilidae, Cecidomyiidae, Chironomidae, Dixidae, Orphnephilidae, Simuliidae, Ceratopogonidae, and Culicidae. The Scatopsidae have the complete pattern with an extra eleventh dorsal anastomosis. It is of interest to note that taxonomic work on external adult features in the Diptera has shown considerable radiation amongst the same nematoceran families as in group (b) above (Crampton, 1942). The fact that the Brachycera and Cyclorrhapha and several families of the Nematocera have retained the complete 'basic pattern' makes the variations in the second group of greater signficance.

Cyclorrhapha

The tracheal system of the Cyclorrhapha (Fig. 1C) is characteristic and is

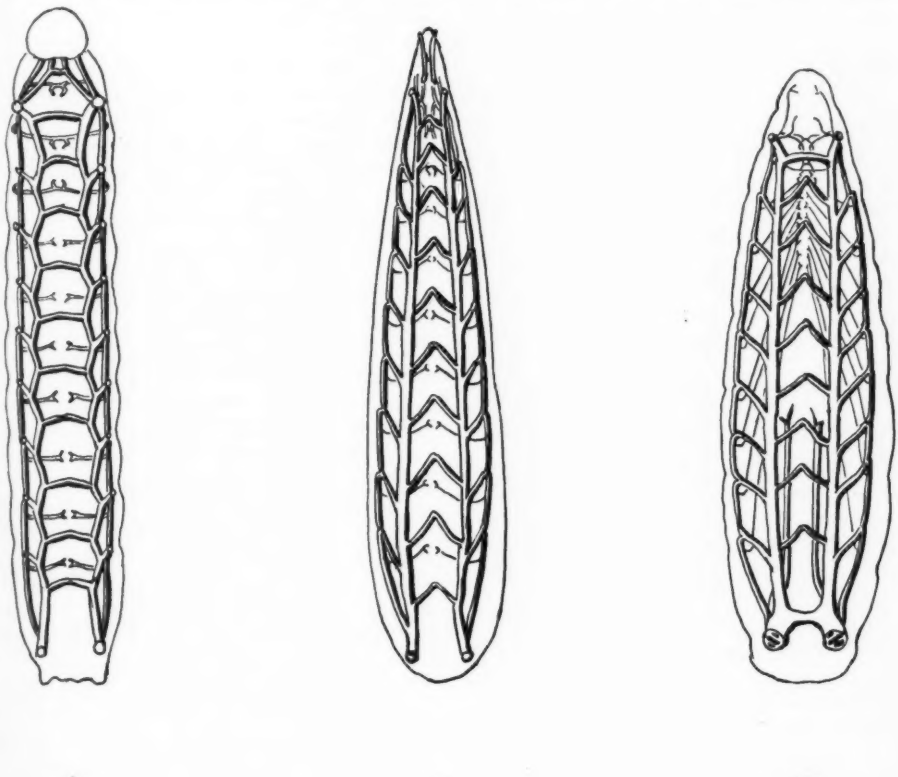

FIG. 1. Dorsal views of the larvae of A) a basic nematoceran tracheal system such as that of *Dilophus febrilis* (Linnaeus) (Bibionidae), B) a typical brachyceran system in which the nervous system is not concentrated, and C) a typical cyclorrhaphan system. All three possess the complete complement of tracheae which constitute the ancestral dipteran pattern.

easily distinguishable from a brachyceran or nematoceran system, even though each may possess the complete pattern. The arrangement of the dorsal and ventral cervical tracheae, the characteristic broad first dorsal anastomosis and shorter broad last dorsal anastomosis, the concentrated nervous system with correspondingly displaced ventral ganglionic tracheae, and the extensive last visceral tracheae are constant features. The system in the Phoridae is typically cyclorrhaphan (Whitten, 1955). The system in the Lonchopteridae is also similar to that of other Cyclorrhapha, except that the last dorsal anastomosis is long rather than short and broad; the larva of *Lonchoptera* (Whitten, 1956b)—the only genus in the family—is so curious in shape that surprisingly the tracheal system is much like that of the more stereotyped cyclorrhaphan larvae. With respect to the tracheal system, the Cyclorrhapha are a homogeneous group; the only deviation from the 'basic pattern' yet seen is the reduction in the second and third dorsal anastomoses in the Syrphidae.

Brachycera

Families of Brachycera that have been studied include the Tabanidae (Whitten, 1956a), Stratiomyidae, Dolichopodidae, Asilidae, and Leptidae (Fig. 1B and Table 1). In each case the 'basic pattern' is complete, except in the Tabanidae where the second and third dorsal anastomoses are reduced. Unlike the Cyclorrhapha, there is no characteristic form to the tracheal system. For instance, there is no differentiation of the first and last dorsal anastomoses; instead, all the anastomoses are usually of a uniform appearance. In the Brachycera with a condensed nerve cord the tracheae are correspondingly displaced; in forms where it is not condensed the ventral ganglionic tracheae and the whole tracheal system have a nematoceran appearance. There are no obvious diagnostic features which could separate the brachyceran tracheal systems from those of the Nematocera.

Nematocera

The Nematocera possess, on the one hand, families in which the 'basic pattern' is retained and where there is little, if any, intrafamily variation. Other families have deviated from the ancestral condition, and show different types and degrees of variation.

The Bibionidae (Fig. 1A) possess all ten functional spiracles and the complete pattern of tracheae; they would seem to have a tracheal system more closely approaching the hypothetical ancestral pattern than other Diptera so far examined. It is quite possible that more tracheae were present in the early dipteran pattern than has been given in the 'basic pattern' for the order. This applies particularly to the anterior end, where, in many Diptera, there are several tracheae of apparent importance that have not been included in the 'basic pattern' because it is uncertain whether they are primitive or 'secondary' developments. For instance, there are in several families of the Nematocera ganglionic tracheae arising from the dorsal cervical tracheae (*dc*) posterior to the dorsal cervical anastomosis (*dca*). These occur in the Tipulidae (Fig. 4), Psychodidae, and Anisopidae (Fig. 2D), although they may not be homologous in all three. In the Tipulidae there are also examples of 'extra' tracheae arising from the ventral cervical tracheae (*vc*) and passing to the supra- and subesophageal ganglia (Fig. 4). Finally, there is the connection between dorsal and ventral cervical tracheae (*d-vc*) seen in some Tipulidae (e.g. *Pedicia rivosa* (Linnaeus), Fig. 2C), the Anisopidae (Fig. 2D), and several aquatic families (Figs. 2A and 2B). Detailed work within these families and a closer study of the head capsules of the remaining nematoceran families should prove instructive. These 'extra' tracheae to the nervous system, and also the dorsoventral cervical anastomosis, if present in the ancestral

TABLE 1

FAMILIES	SPIRACLES	LATERAL TRUNK	DORSAL ANASTOMOSES	VENTRAL ANASTOMOSES	PECULIARITIES
Bibionidae	10	C	1–10	3	
Scatopsidae	9	C	1–11	3	
Anisopidae	2	C	1–10	3	*d-vc* anastomosis
Psychodidae	2	C	1–10	3	
Trichoceridae	2	C	1–10	3	
Brachycera	2 or 1	C	1–10	3	
Tabanidae			2 and 3 absent		
Cyclorrhapha	2 or 1	C	1–10	3	
Syrphidae			2 and 3 absent		
Tipulidae					much intrafamily variation
Limoniinae	1	C	2 and 3 absent 11th present in some: 2–9 absent in Pediciini	3	double anastomosis between *dca* and *da 1* in some
Tipulinae	1	C	2 and 3 absent	3	
Mycetophilidae					much intrafamily variation
Mycetophilinae	8	C	2 and/or 10 absent	2 (3 absent)	
Ceroplatinae	0	C	2–5 and 10 absent	3	peculiar in many respects
Sciarinae	8	Reduced after spiracle 3	1–9 absent	2 (3 absent)	constant for subfamily
Cecidomyiidae	9	C	1–3 absent (1–9 absent in some. 11 present in some)	3	much intrafamily variation
Culicidae	1	C	1 and 3 absent	0	*d-vc* anastomosis; 'gill' tracheae
Dixidae	2	C	1–10	0	'gill' tracheae
Orphnephilidae	2	C	1–10	0	pro-leg tracheae; 'gill' tracheae
Simuliidae	0	Reduced	4–10 absent	0	*d-vc* anastomosis
Ceratopogonidae	0	Reduced	1–10	0	*d-vc* anastomosis pro-leg and 'gill' tracheae
Chironomidae	0	Reduced	1–2 only	0	*d-vc* anastomosis; pro-leg tracheae

d-vc = dorsoventral cervical; *dca* = dorsal cervical anastomosis; *da 1* = first dorsal anastomosis; C = complete.

Diptera, have been lost in the course of evolution of the system leading towards 'higher' more specialized Diptera. These possible ancestral characteristics are absent in the Brachycera and Cyclorrhapha. The only nematoceran family in which it is certain that these elements are absent is the Cecidomyiidae, in which no head capsule is present. In other Nematocera detailed examination of the tracheae within the head capsule is necessary. An eleventh dorsal anastomosis (*da 11*), seen in some Tipulidae (Fig. 3A), some Cecidomyiidae (Fig. 3B), and in the Scatopsidae (Fig. 3C), may similarly be a primitive rather than a secondary feature.

Families Showing Intrafamily Variation. Of the very many dipteran families

FIG. 2. Anterior end of various nematoceran larvae showing the dorsoventral cervical anastomosis. A) *Simulium erythrocephalum* (Degeer) (Simuliidae): dorsal view. B) *Chironomus dorsalis* Meigen (Chironomidae): right lateral view. C) *Pedicia rivosa* (Linnaeus) (Tipulidae): left lateral view. D) *Anisopus fenestralis* (Scopoli) (Anisopidae): dorsal view.

it would probably be found, even after more extensive study, that the only Diptera showing significant variations are members of the Mycetophilidae, Cecidomyiidae, Tipulidae, and the various aquatic families of the Nematocera. Variations that do occur are therefore all the more significant. The main purpose of the present paper is to suggest that as evidence accumulates, these variations will be found to reflect phylogenetic relationships.

Family Mycetophilidae. In the Mycetophilidae, the tracheal systems of members of three of the subfamilies have been described (Whitten, unpubl.). Of these, the Mycetophilinae and Sciarinae are hemipneustic, whilst the Ceroplatinae are apneustic. The Sciarinae have a remarkably constant tracheal system, as all species seen to date have an identical pattern. On the other hand Mycetophilinae, Ceroplatinae, and, as far as has been determined, the other subfamilies, display considerable variation.

Sciarinae: The tracheal system is characteristically reduced. Only the tenth dorsal anastomosis remains, and the lateral longitudinal trunks are absent posterior to the third spiracular tracheae. The only oddity which the tracheal system possesses in common with any other mycetophilids is the absence of the third ventral anastomosis, which is also absent in the Mycetophilinae studied, e.g. *Mycetophila cingulum* (Meigen). Although the same variation can occur in obviously unrelated groups (for example the loss of dorsal anastomoses two and three in some Tipulidae, Tabanidae, and Syrphidae), the three ventral anastomoses are present in *all* Diptera studied except Sciarinae, My-

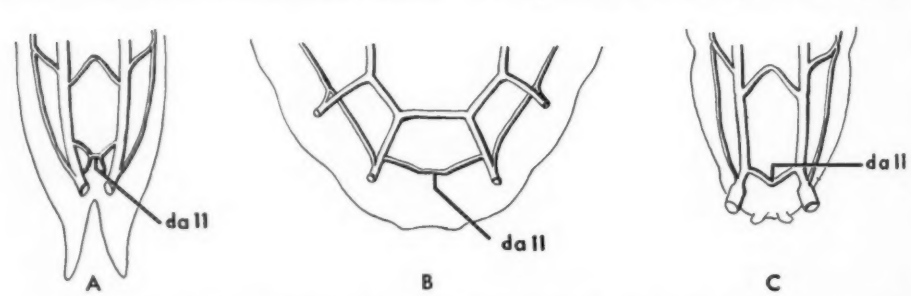

FIG. 3. Dorsal view of the posterior end of A) *Dicranota bimaculata* (Schummel) (Tipulidae), B) unidentified members of the Cecidomyiidae, C) *Scatopse notata* (Linnaeus) (Scatopsidae). All possess an eleventh dorsal anastomosis situated anterior to the last pair of spiracles.

cetophilinae, and the aquatic families; in the latter case all three are absent. This variation cannot be ignored or automatically dismissed as due to convergence. Within the Sciarinae there has been found no variation from the subfamily pattern, and on the basis of the tracheal system it would appear a homogeneous group. Some dipterists would separate the Sciarinae from the rest of the Mycetophilidae (e.g. White, 1949). Certainly the sciarid tracheal system is distinct and shows no resemblance to that of other mycetophilids, with the one exception of the third ventral anastomosis discussed above. If the tracheal system has diverged from a common mycetophilid stock, it has subsequently remained hemipneustic and retained a stable though reduced pattern.

Mycetophilinae: The system in this subfamily is complete except for the absence of the third ventral anastomosis. Variations within the subfamily involve the dorsal anastomoses. In some cases the second is reduced, in some the tenth, and in others the second and tenth.

Ceroplatinae: The only member of this subfamily that has been described and identified is *Ceroplatus testaceus* Dalman. Not only is the system apneustic, but internally it is remarkable in appearance (see Table 1). Other Ceroplatinae and Bolitophilinae have been observed though not identified: further variations are evident, so that one may anticipate an accumulation of evidence that may prove of future systematic interest.

Family Cecidomyiidae. In all Cecidomyiidae examined, and in those described by others (Metcalf, 1933; Otter, 1938; Williams, 1910) dorsal anastomoses one, two, and three are always absent. The full complement of other elements is present. The larvae are peculiar in the lack of a head capsule, and in the concentration of the nervous system, thus giving the tracheal system a characteristic appearance. There is further intrafamily variation involving the dorsal anastomoses: in some Cecidomyiidae there is only one dorsal anastomosis; this condition is seen in the dasyneurine *Taxomyia taxi* (Inchbald). In other genera, including *Clinodiplosus, Lestodiplosus,* and *Cecidomyia* of the Cecidomyiini dorsal anastomoses four to ten are present. An eleventh dorsal anastomosis is present in some Cecidomyiidae (Fig. 3B); here two anastomoses lie between the ninth and tenth spiracles. The possession of a particular variation in the dorsal anastomoses may well signify a common relationship in this family. It is a large family with many subdivisions, and the tracheal system could serve a useful purpose in determining the particular segregate to which an individual belongs, *if* it can be accepted as a reliable taxonomic character. Only more research within the different subdivisions can verify its reliability in dipteran taxonomy.

It is of particular interest to note that Hennig (1952) also considered the number of dorsal anastomoses to be of possible systematic value in the Cecidomyiidae. In

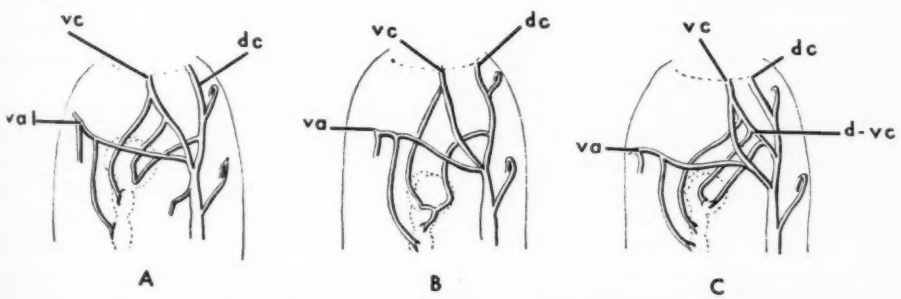

FIG. 4. Left lateroventral view of the anterior end of various Limoniinae showing some of the variations in the tracheation of the supra- and subesophageal ganglia in this subfamily.

practice, the number of anastomoses could be determined in any larva in a matter of seconds by placing the larva in water between slide and cover-slip, and viewing through the transparent body wall.

Family Tipulidae. The Tipulidae exhibit considerable intrafamily variation. Unfortunately, no member of the Cylindrotominae has been studied, but many examples of the Tipulinae and Limoniinae have been described (Whitten, unpubl.; Wardle, 1926). On cytological evidence White (1949) suggested separating the Limoniinae from the Tipulinae. The tracheal pattern of the two subfamilies would not support this separation, as the basic patterns of the two resemble each other more than they do any other dipteran system (Table 1); in both subfamilies the pattern is complete except for the absence of dorsal anastomoses two and three. Also, there is the same complexity of branches to the supra- and subesophageal ganglia, and members of both are metapneustic.

Tipulinae: It is significant that the Tipulinae examined show little variation, for all the members so far studied have almost identical tracheal patterns. This is consistent in that the subfamily is, in Britain, made up of only seven genera, whereas the Limoniinae are subdivided into four tribes, the Limoniini, Pediciini, Hexatomini, and Eriopterini, all containing many genera.

Limoniinae: In contrast to Tipulinae, the Limoniinae show considerable variation. Tracheation to the supra- and subesophageal ganglia shows many small, but distinct, differences in number and distribution of tracheae arising from the cervical tracheae (Fig. 4). The curious double anastomosis, described for *Austrolimnophila ochracea* Meigen, has been observed also in other unidentified limoniid larvae. Again, there is variation found in the dorsal anastomoses (*da*); in *Pedicia rivosa* and *Dicranota bimaculata* (Schummel) the dorsal anastomoses are reduced to the first and last, and they both possess an eleventh dorsal anastomosis (Fig. 3A: *da 11*), from which arise branches passing to the 'gills.' The genera *Pedicia* and *Dicranota,* on adult characteristics, are placed in the Pediciini, together with a third British genus—*Ula.* It is therefore hardly coincidental that their tracheal patterns should be almost identical and different from other limoniids studied. These variations within the Limoniinae, although many, would seem to be consistent, and almost certainly reflect phylogenetic relationships. More work is necessary to confirm this hypothesis.

Aquatic families. Of particular interest are the aquatic families of Nematocera. These include the Culicidae, Dixidae, Orphnephilidae, Chironomidae, Ceratopogonidae, and Simuliidae. They are the only Diptera in which all three ventral anastomoses (*va*) are absent (see Table 1). Also, in all except the Dixidae and Orphnephilidae the characteristic dorsoventral cervical anastomosis is present (Figs. 2A and 2B). The 'gills' are tracheated in a similar manner in the Culicidae, Dixidae and Orphnephilidae (Fig. 5:*gt*): a trachea arises from the lateral trunk of either side, near the posterior spiracles (*sp*), and divides to pass to the two 'gills' of that side. Since the lateral trunks are absent at the posterior end in the Chironomidae, Ceratopogonidae, and Simuliidae, it is not possible to homologize the 'gill' tracheae of these families with those of the Dixidae, Orphnephilidae, and Culicidae, but Figure 5D suggests a similar origin in the Ceratopogonidae. It may also be significant that the prothoracic leg tracheae have identical origins in the Chironomidae, Ceratopogonidae, and Orphnephilidae (Fig. 6, A, B, C).

The tracheal patterns of the Dixidae and Orphnephilidae are almost identical, possibly a characteristic suggesting the grouping of the Orphnephilidae near Dixidae, rather than near Chironomidae (*cf.* Keilin, 1944). On adult characteristics the Dixidae are usually placed with Culicidae; they are sometimes included with the Culicinae and Chaoborinae as a subfamily

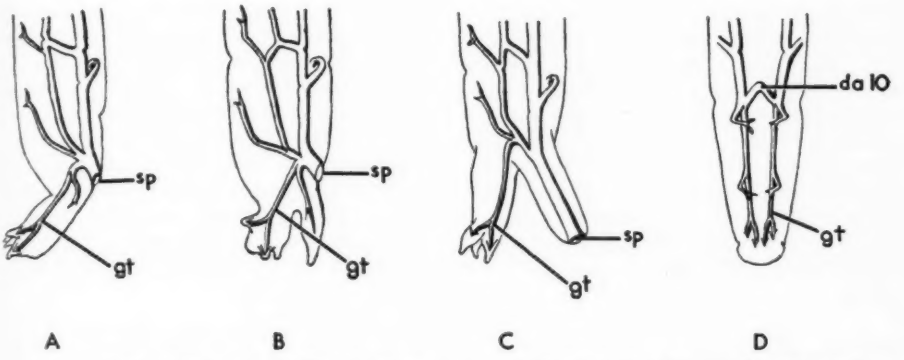

FIG. 5. Left lateral view of the posterior end of various aquatic larvae showing the origin of the 'gill' tracheae. A) *Orphnephila testacea* Ruthe, B) *Dixa (paradixa) autumnalis* Meigen, C) *Culex molestus* Forskal, D) *Culicoides* sp., dorsal view.

of the Culicidae. The tracheal systems of Dixidae and Culicidae differ in that the last instar of the former is amphipneustic and the latter metapneustic; also, the dorsal anastomoses are complete in the Dixidae, whereas numbers one and three are absent in Culicidae. On the other hand, Dixidae and Culicidae have several common characteristics with regard to the tracheal system. These include the complete lateral trunks, characteristic 'gill' tracheation, and presence of functional spiracles.

The Chironomidae, Ceratopogonidae, and Simuliidae are all apneustic and have reduced lateral trunks. In the first two families the lateral trunks are present as far as the third spiracular trachea, whereas in Simuliidae reduction has gone farther, as the lateral trunks extend only between the first and second spiracular tracheae. In the Ceratopogonidae all ten dorsal anastomoses are present, whereas these have been reduced to three in the Simuliidae, and one or two in the Chironomidae. In the Simuliidae there is intrafamily variation involving reduction of the dorsal trunks at the posterior end, and in

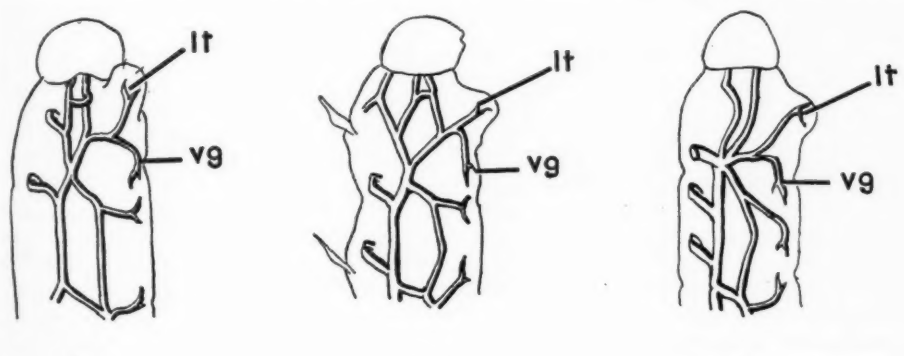

FIG. 6. Right lateral view of the anterior end of various aquatic larvae to show the prothoracic leg tracheae. In each case the trachea arises from the first ventral ganglionic trachea. A) *Chironomus dorsalis* Meigen; B) *Forcipomyia* sp.; C) *Orphnephila testacea* Ruthe.

Chironomidae there is intrafamily variation which takes the form of reduction of both the dorsal anastomoses and the posterior end of the system. Stuart (1941) correlated tracheal reduction and haemoglobin presence, but gave insufficient details of the tracheal system. Of the aquatic families, the Chironomidae would probably be the most rewarding to study in detail, and it is likely that results of systematic and physiological interest would emerge.

Conclusions

Much detailed work remains to be done on the individual families in which variations occur. The present paper is intended to indicate where more intensive study could, in all probability, be profitably made. In cases where a variation in the tracheal system is found to be of taxonomic value, this could be easily ascertained, as most of the larvae of the Nematocera are transparent. The tracheal system may then be of practical use, since many of the larval Nematocera are impossible to identify without breeding through to the adult stage. It has not been the object of the present study to homologize any 'secondary' tracheae, but to concentrate on the fundamental framework which is made up mainly of longitudinal and transverse connections, together with important tracheae such as the spiracular, ganglionic, and head tracheae. The 'additional' tracheae may well be of importance at the generic or specific level. The reputed instability of the tracheal system is largely due to confusion between secondary tracheae and more fundamental tracheal 'connections'; it is chiefly the latter which characterize and constitute a particular tracheal pattern. Wigglesworth (1954) has demonstrated that new tracheae will grow into an area requiring oxygen, such as a new implant, but this has not demonstrated any alteration of the basic framework which exists.

A separate study is under way of adult tracheal systems as well as the development of the system in the different dipteran families. These all provide evidence of the stages through which the tracheal system has passed in its evolution from the basic ancestral condition to its present form in the various groups of Diptera. Each separate field of study confirms the basic stability of the system and its potentialities as a taxonomic character, and also indicates its value for systematic work in helping to determine possible phylogenetic relationships.

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Mendelian Infraspecific Divergence Levels and their Analysis

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DIAGNOSED Mendelian subspecies often contribute little more than scientific names to the literature; in general, they are populations of unknown evolutionary significance. This variance with the spirit of the "new systematics" results from acceptance of procedures that name subspecies first and supposedly consider relationships later. Because the emphasis is on naming, rather than determining relationships, present practices might be more a hindrance than a contribution to knowledge. For example, accepted systematic methods are such that any variant within a species might be given a subspecies trinomen—even ecophenotypes and polymorphic forms can be accorded subspecific rank. The probable results of these and other practices were aptly summarized by a colleague's statement, "Present systematic practices are creating more problems than the next generation of systematists can solve." These practices have caused many systematists to reject the subspecies, yet evolutionary theory might benefit tremendously by a meaningful subspecies concept. The evolutionary relationships within a species, whether they be considered phylogenetically or statically, and reasonable methods for their analysis are the primary considerations of this paper.

The subspecies problem is related to the levels of divergence that can be found within species. It is generally accepted that examples of every conceivable "point" along the path of speciation occur in nature. This premise seems valid even if a single path, or process, exists only in the sense that isolation and genetic change constitute "the process." The bases for the premise are the many examples of different subunits of various species that seemingly indicate a complete range of divergence, i.e., "points" along the path of speciation. In other words, it is generally believed that one can find a complete gamut of the results of evolution, from species with subunits showing insignificant deviation to species with subunits that border on being species themselves. This, of course, is a necessary corollary to the generally accepted beliefs on the mechanisms of speciation.

Although levels of divergence are almost universally accepted, subspeciation studies tend to ignore these levels. It is agreed that certain minor patterns of variation, e.g., microgeographical, microecological, and microchronic races, may show low divergence. However, such variation seems to be rarely studied and, if discovered, it is rarely mentioned. Mysteriously, these microraces are beyond the scope of most studies, and are not often found. In fact, one often gets the errone-

ous impression that such studies might be of little use. At the same time, other patterns of variation, that are usually incapable of being accurately defined in actual studies, supposedly show "high" levels of divergence. These rather nebulous entities are frequently called "subspecies," given a trinominal designation, and considered very valuable contributions to the knowledge of a particular species. This appears to be the case even though the levels of divergence are generally undefined, often impossible to diagnose from the data available, and usually not specified when such "subspecies" are named.

Few investigations of speciation consider the entire pattern of variation within the species as a whole. Too often a few specimens from a single locality are awarded a trinomen on no basis other than a statistical difference between these specimens and previously known specimens. The fallacy in this practice has already been emphasized (Pimentel, 1958). In even less precise methods, a consistent difference is observed in a few specimens, and without reference to statistical probabilities, a new "subspecies" is named. In "more critical studies" certain patterns of variation within the entire species might be indicated, e.g., clines and step clines. The various clinal and step clinal variations are used to delimit "taxonomically distinct" populations. Each of these demes is then named as a "subspecies." In such instances the relative difference between graded clinal and step clinal levels of divergence are not usually considered. Finally, current acceptable practices might allow different phenotypic expressions of identical genotypes to be named as different "subspecies." This might be exemplified by many of the subspecies known only from a type locality that is remote from the rest of the species or that lies within the range of another subspecies.

The above indicates that many named "subspecies" contribute little to our knowledge of relationships within species. Yet, after general disrepute of the "old systematics," the "new systematics" supposedly rejuvenated the science by emphasizing evolutionary relationships. If neo-Darwinism is to be emphasized, it seems that levels of divergence *must* be recognized and defined, and convenient methods of analyzing these levels should be made available.

In the first section of this paper five levels of divergence are proposed for recognition. Five levels are used because they seem to be the most that can be distinguished with our present knowledge and methods, and at the same time they are sufficiently precise to enable us to clearly describe most infraspecific variation. The final portion of this paper emphasizes the inadequacy of present systematic procedures and provides methods for analyzing levels of divergence.

Levels of Infraspecific Variation

Although different levels of infraspecific divergence are recognized by most workers, only Edwards (1954) and Van Son (1955) have attempted to associate a subspecies concept with these levels. The present treatment subscribes to Edwards' subspecies definition: Subspecies are natural, obviously different entities (he originally used the word populations), the members of which would crossbreed rather freely *if* they occurred sympatrically and synchronically under natural conditions, *but which are distinctly separated during their mating periods* (with the result that they do not normally crossbreed). Edwards did not define what he meant by "obviously different" entities. Although he did decry subspecific rules *without biological criteria* he does admit (pers. comm.) the need for some more precise means of defining "obviously different." This definition only considers the highest level of infraspecific divergence as being worthy of the description as "subspecies." Edwards did not treat levels below the subspecies except to supply the term *morph* for sympatric, synchronic

demes with recognizable differentiating features. Levels of divergence, including the subspecies level, are emphasized in the following section. Also, a method of using Edwards' subspecies definition in practical problems is proposed. It is hoped that this may reconcile the proposed interpretation with earlier criticisms of the broad, or undefined, subspecies concept.

Infraspecific Divergence Levels. Five important questions need to be answered: (1) Are present ideas about patterns of variation accurate? (2) If not, what are the true patterns? (3) Can true patterns be reduced to generalizations, e.g., graded clines, step clines, morphs, subspecies, etc.? (4) How long do patterns of variation persist? (5) Are patterns of variation similar among sexually reproducing species in different phyla?

Although acceptance of neo-Darwinian generalizations is basic to the following discussion, the section on analysis is not so limited. The proposed methods of study are just as valid for discovering unknown patterns of variation that might exist as they are for disclosing presently accepted patterns.

Any definition of levels of divergence must be somewhat arbitrary because there are probably multi-dimensional paths to speciation. We cannot say with certainty that speciation always proceeds through definite patterns of variation, e.g., clinal, scattered, step clinal, etc. This, however, does not prevent systematists from loosely delimiting artificial levels of divergence, if these levels conform with theory by indicating possible significant steps heading toward speciation and providing bases for measurement. Without recognized levels that are capable of being tested there seems to be little hope of resolving the present confusion about subunits of the species. Finally, arbitrary procedures should not, by themselves, be a reason for rejecting these levels, because the same sort of arbitrariness occurs in our delimitation of species (Clark, 1956).

Various patterns of variation certainly exist in nature. Some of these patterns are illustrated in Figure 1. The abscissas in these diagrams represent location or distribution in the broad sense (geographical, ecological and temporal); the ordinates represent the mean value for a single character. These diagrams are here simplified to the extent that location contains length but no width; and combinations of factors, such as geography and time, are ignored. In the top half of Figure 1 various continuous distributions are indicated; in the lower half, various discontinuous distributions. These diagrams might be representative of most conditions found in nature, but is probable that they underestimate the complexity that does exist. Their only purpose is to serve as a guide in designating arbitrary levels in a continuum of variability.

The following levels of divergence seem most significant: subspecies (in the strict sense), step clines, scattered or irregular variation, gradual or graded clines, polymorphism, and uniform variation. However, this is an oversimplification because countless complexities of variation patterns undoubtedly exist. For example, secondary intergradation might assume the appearance of any of the more complex clines. In Edwards' subspecies definition, considerable importance was given to discontinuous distribution. Below his proposed "subspecies level," isolation assumes variable importance. Surely uniform discontinuous distribution does not represent as high a level of divergence as any step cline pattern. An additional problem is reproductive isolation between remote subunits *within* a species, even though these subunits are linked together by series of interbreeding populations. Where do they fit into levels of divergence?

Perhaps a mere description of observed variation *below* the stringent subspecies level might be the best solution. This should present a detailed analysis of the variation patterns, and one could refer to trends in variation by descriptive adjec-

tives, e.g., polymorphic, uniform or graded clinal, step clinal, etc. On the other hand, even an arbitrary segregation of levels, if it indicates the steps in the speciation process, seems justified. This might lead us away from the present tendency to ignore differences in the amount of divergence, either when naming subspecies or in criticizing the subspecies concept. The major problem in the placement of levels is probably the position of scattered variation.

The following levels are easily recognized: I. continuously distributed, homogeneous species with uniform infraspecific population variation (Fig. 1: a); II, discontinuously distributed homogeneous species with uniform infraspecific variation (Fig. 1: i); III, continuously distributed species with (IIIa) graded clinal (Fig. 1: b), (IIIb) step clinal (Fig. 1: d), and (IIIc) irregular or scattered variation (Fig. 1: c, e, f, g, and h); IV, discontinuously distributed species with (IVa) graded clinal (Fig. 1: k), (IVb) step clinal (Fig. 1: l and m), and (IVc) irregular variation (Fig. 1: j, n, o, and p); and V, the subspecies as herein considered.

Two phenomena are considered to represent special cases and not true levels of divergence. The first is polymorphism which fits level I despite the variability (for there *is* "uniform infraspecific variation" and no more problem should arise here than in the more common examples where there is "sexual dimorphism" to complicate matters.) The second is reproductive isolation between *remote* subunits within a species. This can occur in either continuously or discontinuously distributed species, either having a linear or a circular distribution pattern. The terminal populations within a single species having any of these distributional characteristics are sometimes reproductively isolated. Moore (1944) discusses the linear type and Stebbins (1957), the circular type. In both cases gene flow is continuous through other demes of the species.

No subspecies (or species) definition ever presented is without subjectivity when it comes to measurement in the field. Moreover, it is not likely that a definition can be developed that will eliminate this shortcoming. The following discussion will attempt to indicate why the proposed subspecies interpretation results in a less arbitrary category than do other definitions.

Many patterns of discontinuous distribution were discussed and figured. Although subspecies were not considered in the figure, some of the discontinuous patterns seem similar to those that might be found in "good subspecies." Edwards' spatially, temporally, and/or ecologically isolated "obviously different populations" are limited to distinct morphological, behavioral, and/or physiological *disjunctions* from adjacent populations. This provides an approach to a non-arbitrary subspecies. In the figure, only l shows clear disjunction among the groups of populations. These seem to be obvious subspecies even though the diagram represents a simple type of discontinuous step cline. An example of such a pattern might be found in the long-toed salamander, *Ambystoma macrodactylum* Baird. Recently (Russell and Anderson, 1956) 22 adults were found 400 miles south of the known California Coast Ranges locality and 150 miles southwest of the nearest known Sierra Nevada populations, from which the new population is separated by the Great Central Valley. The new subspecies possesses certain consistent differences from other populations. Also, sufficient specimens were obtained for reliability in measuring amount of divergence. Although this new form might have been considered a distinct species, the authors give valid reasons for subspecific treatment. A number of such morphologically distinct populations that are isolated from the rest of their species are known among the amphibians and reptiles of western North America (Stebbins, 1954). Further examples seem to be indicated by Hall and Kelson (1959) in North American mammals. It is doubtful that all of these seemingly distinct forms could merely be ecophenotypes—especially

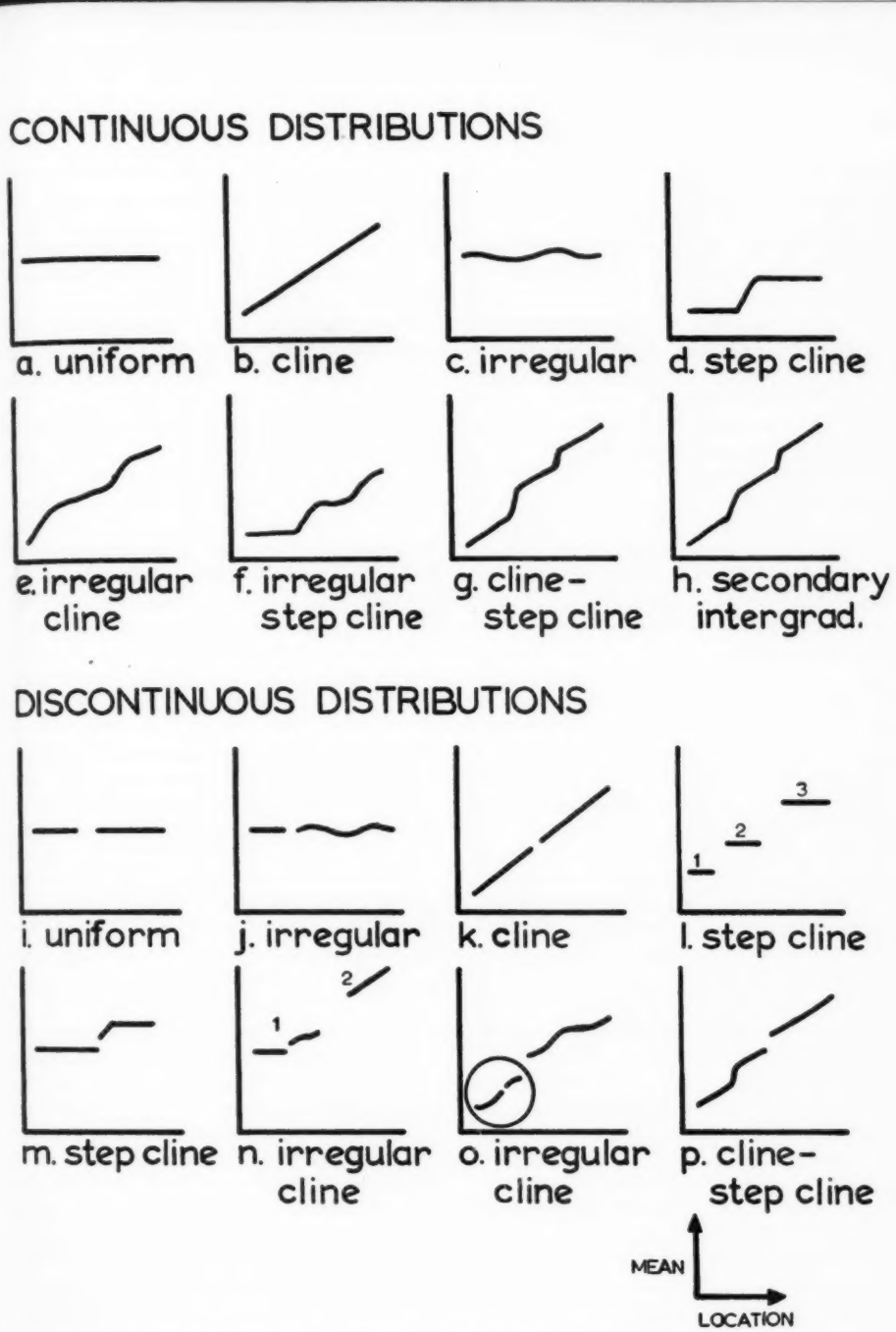

FIG. 1. Some patterns of infraspecific variation in single characters (simplified). The upper diagrams (a through h) are examples of generalized variation patterns in continuously distributed species; the lower diagrams (i through p), of patterns in discontinuously distributed species. Distribution disjunctions in the latter patterns indicate either geographic, ecological, or temporal barriers.

those possessing a number of unique characters, and, certainly no disadvantage can result from applying trinominals to these isolates instead of calling them "different species."

This highest level is easily recognized on theoretical grounds (Edwards, 1954). It, of course, is closely effected by the process of speciation because of the possibility of genetic change during any isolation between breeding-stock. Physical isolation, be it either temporal, geographic, or ecological (=microgeographic), has the same effect on the population gene-pool. Genetic changes in such populations usually occur independently from the general pattern of variation in the rest of the species. Because such populations already display genetic divergence and, due to isolation, are likely to continue to diverge, they could be considered "potential incipient species" (Mayr, 1942). Such populations should be the only ones designated subspecies, according to Edwards (1954), Van Son (1955), and the author.

This proposal is subject to many arguments. Perhaps the two most obvious result from the references to "genetic divergence" and "potential incipient species."

Quantitative expression of genetic divergence must, to some extent, be arbitrary. It is not desirable that every isolated, divergent population should qualify as subspecies. Camin and Ehrlich (1958) give examples of such poorly differentiated demes in the common water snake, *Natrix sipedon* (L.). In the figure certain patterns would be immediately rejected as subspecies because no isolated subunit shows sufficient character divergence from the rest of its species (Fig. 1: i, j, k, m, and p). In contrast to this, certain patterns have subunits that should definitely qualify as subspecies (Fig. 1: l and n, as numbered). However, Figure 1, o emphasizes that the proposed subspecies interpretation does not eliminate all of the problems of interpreting amounts of genetic divergence. The lower group of circled populations may or may not constitute a single subspecies. For situations like this, it seems necessary that some minimum amount of physiological, physical, or behavioral divergence be considered necessary and that this divergence be found in a number of independently segregating, genetically independent characters. An 84 percent from 84 percent segregation might be acceptable *if* one's methods of study could assure that this much divergence actually occurred (Pimentel, 1958). In actual practice, because of the restrictions in the definition of this proposed "subspecies," it seems that more than one character could be found to diagnose this level. In fact, it is likely that many characters would separate 100 percent of the isolated populations from other populations of the species *if* the physical isolation is complete (as required by the definition). Because of the difficulty of obtaining measurable morphological, physiological, and behavioral characters in some groups of animals, one cannot state exactly how many characters should always be found to segregate subspecies. This must be left to the discretion of the systematists of each group of animals, and may be interpreted as "taxonomic sense" if judiciously applied.

Much confusion is associated with the use of subspecific rules. *First,* individual usages of percentages have been interpreted to designate entirely different amounts of character overlap between so-called "subspecies" (Mayr et al, 1953). It is here assumed that any percentage prefixing a rule defines the point of intersection of the two "populations" being compared. This would mean that a 75 percent rule would consider as minimum character divergence 75 percent disjunction of one population from 75 percent of the other. *Second,* even after acceptance of the point of intersection of two curves, the actual percentage of segregation can be stated in different ways. For example, a 75 percent rule would indicate all of the following: (1) 5 percent from 99.9 percent, (2) 10 percent from 99.5 percent, (3) 25 percent from 99 percent, (4) 50 percent from 92 percent, and (5) 75 percent from 75 percent. All of these interpretations

can result from the fact that two overlapping "normal" curves can be considered to display their overlap in many different ways. *Third,* most calculations to determine the point of intersection of the two curves are unreliable. A reliable method has been proposed (Pimentel, 1958).

Selection of a particular percentage for a rule is not a simple matter. Choice must be based on both theory and practical considerations in the field. Theory, at the present time, gives us little information about any expected lower limit several characters can be expected to assume and still diagnose a fifth level subspecies. In many cases, demes conforming to the proposed subspecies definition appear to show 100 percent divergence in a number of traits from other subunits of their species. However, even if one believed all subspecies should show such distinction, statistical "proof" of this is often impossible —in general, "proof" would necessitate fantastically large numbers of organisms. Perhaps this is sufficient to indicate that any rule is in a sense conservative—divergence will often be *more* than indicated by any *reliable* subspecific rule. The important consideration is that, at the very least, a reliable rule (with only slight possibility of error) indicates minimum possible divergence, or, conversely, maximum possible overlap in characters (75 percent indicating that 25 percent of each population overlaps the "distinct" 75 percent of the other). In addition to these practical aspects of using a particular rule, there is reason to believe that many "potential incipient species" might show less than 100 percent divergence in their diagnostic characters. This, of course, indicates the need for an arbitrary lower limit for field diagnosis of a theoretical entity. If it must be arbitrary, consideration of possible percentages (other than 75 percent) is in order.

Four additional percentages will be considered: 84, 90, 95, and 97. A number of interpretations of the divergence indicated by each of these percentages is portrayed (Fig. 2). The relative effect of each percentage can be better appreciated if one considers how many specimens are necessary from *each* of two "populations," one possessing but the other *not* having a particular trait, to have no indication of statistical overlap (95 percent confidence coefficient) when using a particular rule. The percentages and number of specimens are 84 percent, 22 specimens; 90 percent, 35; 95 percent, about 80; and 97 percent, about 150 specimens. Although 95 and 97 percentages produce marked distinctions between populations in comparison with lesser percentages, they also involve sampling to an extent that may be impossible in the field. In addition, there seems to be little real difference (mathematically) between a 90 and 84 percent rule, but there is a marked difference between 84 and 75 percent. Taking these consequences into account, and purely on a basis of opinion, an 84 percent subspecies rule is recommended in this paper. As will be emphasized later, subspecies can be recognized *only* after sampling and study of elements representing the entire species. Moreover, only demes showing disjunction from the pattern of character variation in other subunits of the species should be considered for testing by the rule.

The choice of the "84 percent from 84 percent rule" should satisfy many critics of the broad or undefined "subspecies." Such a level of divergence would curb the tendency to name new species on the basis of a "type" and a few paratypes (Pimentel, 1958). Also, such a level of divergence would not likely occur as a transient genetic change in a localized population. Use of this divergence and the methods already proposed would demand a critical assessment of any population relationships and there should be little doubt about the statistical "significance" of a number of characters, *each* indicating a minimum of 84 percent divergence.

A particular restriction of the term "potential incipient species" is used throughout this paper. One might well argue that any deme, whether completely isolated or not from adjacent populations, constitutes

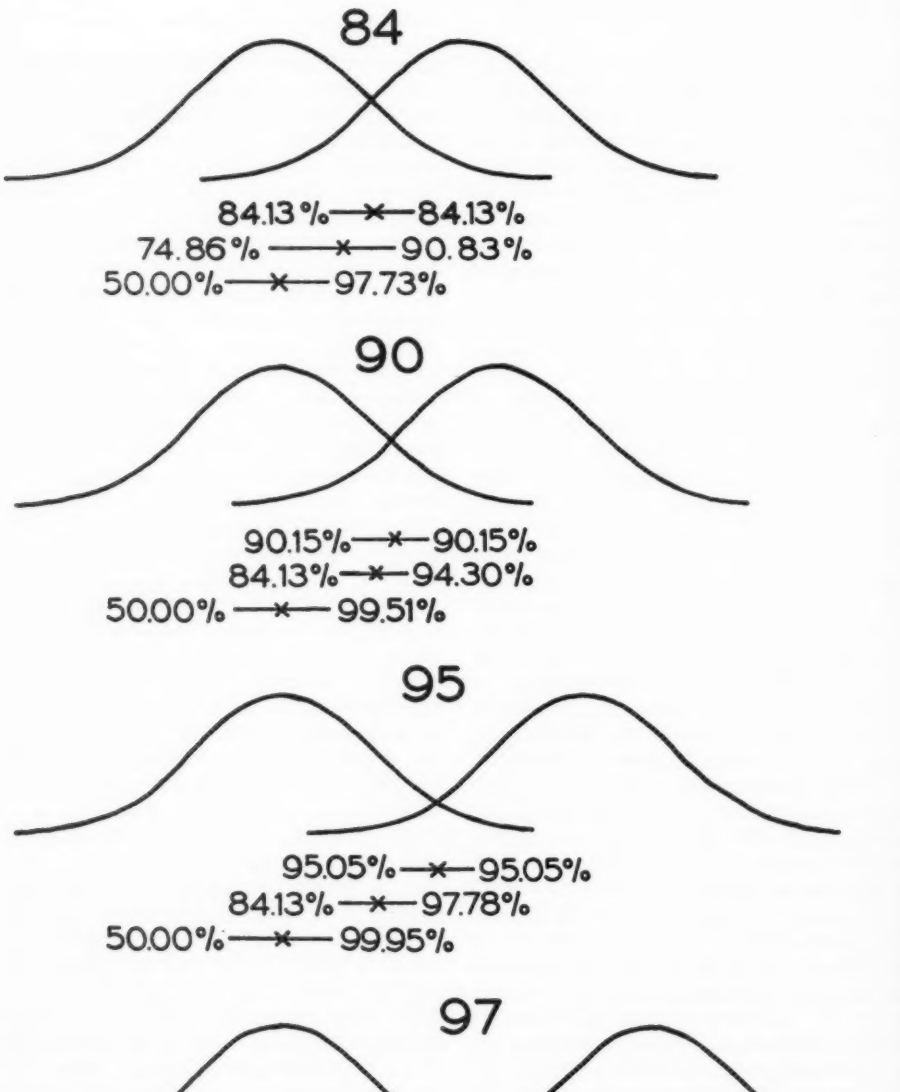

FIG. 2. Intersections of two "Normal Curves" indicating four "Subspecific Rules." The point of intersection of each pair of curves gives the percentile associated with each rule. This point is the only one that delimits equal percentages of segregation between two Normal Curves, i.e., populations. Various interpretations of the amount of segregation indicated by each "rule" are given.

an incipient species. However, until isolation occurs, the likelihood of speciation is remote. Other discontinuous distribution patterns in Figure 1 tend to show continuous trends in single character variation. If no characters show sufficient disjunction, it seems best to consider them infraspecific variations and describe the variation of each of the individual characters. Each character could be graphed and linked with its level of divergence. Such useful data would adequately emphasize relationships within any species.

It should be realized that when an entire species is adequately diagnosed, a group of the populations can represent any of one or more divergence levels. For example, a subspecies (level V) might itself be continuously distributed with its interpopulation variation following a graded cline (level III). Of course, other populations of the species could also display one or more divergence levels. In fact, the discussions of these combinations of levels would emphasize the complexity that conventional approaches usually completely ignore.

This entire treatment has emphasized a subspecies defined on the basis of physical isolation (either geographic, ecological, or temporal) during the reproductive period. Furthermore, these subspecies must show obvious character divergence from the rest of their species in morphology, behavior, and/or physiology. Although most of these subspecies should possess distinction in all three kinds of characters, some may diverge in only one or two of these features. W. J. Brown (1958, 1959) seems to give some examples of this situation. A clear example is found in *Anopheles* mosquitoes in Europe, which are composed of members that appear identical morphologically, but differ in mating behavior and egg structure. Unfortunately at the present time there are few attempts to quantify genetic differences that are not expressed morphologically. However, any biological character that can be observed to display variation can be quantified.

The Subspecies Problem. Systematists, as a result of their investigations, have recognized and named certain infraspecific populations as subspecies. Although the subspecies and trinomen antedate modern evolutionary theory, efforts have been made to make them comply with this theory. However, usage and procedure vary a great deal with the individual systematist. All of these various approaches can be reconciled with the following broad subspecies definition proposed by Mayr (1942, p. 106):

"The subspecies, or geographic race, is a geographically localized subdivision of the species, which differs genetically and taxonomically from other subdivisions of the species."

This definition places little actual restriction on the use of the trinomen. A population, occupying an extremely restricted area and showing a minimum of genetic divergence from other populations of the species, would qualify as a subspecies and for trinominal designation. Some workers have used the broadest interpretation of Mayr's definition and have ignored degrees of genetic divergence. It seems that even microraces and individual variants have been named as subspecies, just because the definition allows it. As a result of this excessive splitting, there is much opposition to the old subspecies concept. Most opposition is against the overabundant use of the trinomen, rather than against the general validity of neo-Darwinian theory. The opponents decry the excessive splitting of certain species, especially examples such as a pocket gopher (*Thomomys bottae*) with more than 150 subspecies described from western North America. Incidentally, many of these may still be valid, according to the restricted definition, because many of these "subspecies" are geographically isolated and show some morphological divergence and character correlation. A few taxonomists suggest that the entire subspecies concept is meaningless and should be discarded. This view has not been exceedingly popular among systematists, possibly because of the great uncharted gaps that would result

in our systematic treatment if every infraspecific entity were lumped together as equally unimportant and treated accordingly.

The remainder of this section summarizes the criticism of broad interpretation of the subspecies and suggestions resulting from this criticism. The criticisms and suggestions are emphasized by being italicized. Comments and/or attempts to justify present views follow the criticisms. The literature cited is not intended to be an extensive coverage.

The following criticisms have been made of the old subspecies concept and the application of the trinomen to such subspecies:

1. *There is no precise definition of subspecies. The concept is applied to various heterogeneous phenomena thereby obscuring relationships* (Edwards, 1954; Gosline, 1954; etc.). This is the basis for discontent with the original, broad neo-Darwinian subspecies as defined by Mayr. These authors are objecting to the ignoring of different levels of divergence.

2. *Too much time is wasted by systematists on subspecific nomenclature* (Gosline, 1954). Nomenclature is a problem at any taxonomic level. A more stringent subspecies concept would simplify the situation.

3. *Subspecies are defined on the basis of differences, while relationships tend to be ignored* (Gosline, 1954). *Analysis is directed toward naming, rather than studying the relationships of genetic characters* (Wilson and Brown, 1953). These seem to be valid criticisms. Although theory is often mentioned in articles, many "subspecies" are named as soon as a new locality is found to harbor members of a species and morphological differences are noted. Surely, such procedures cannot be considered as contributions to evolutionary thought. The widespread criticism that such practices accomplish nothing more than naming unknown phenomena seems justified. Although the infraspecific taxonomic procedures proposed in this article would name subspecies on the basis of constant differences, the knowledge of these differences would result from conscientious studies and would emphasize *relationships* between demes, or populations.

4. *Much of the criticism of subspeciation might be based upon inexact taxonomic methods* (Pimentel, 1958). General taxonomic methods are such that many previously named subspecies would be of doubtful validity even when the old, unrestricted subspecies concept is invoked. These practices are directly related to the third criticism.

5. *Points along gradual clines should not be named as subspecies* (Burt, 1954; Sibley, 1954; etc.). *Microgeographic races* (Brown and Wilson, 1954; Doutt, 1955; Edwards, 1954; etc.) *and rapidly changing, unstable populations* (Fox, 1955) *should not be described as legitimate subspecies.* Many systematists agree with this statement, but the generally accepted, uncritical methods of analysis might still allow such variants to be described as "subspecies." For this reason, it seems to be a problem of analytic methods rather than one of basic beliefs. It is thought that use of the recommended procedures in the second section of this paper will alleviate this difficulty and prevent the description of "undeserving" demes as subspecies.

Many authors have given valid reasons why there should be no justification for the naming of these demes as "subspecies." Their criticisms emphasize the temporary genetic status of points along a cline, vague and incomplete isolating factors, and the resulting lack of sufficient character correlation, i.e., there is nonconcordance of characters. The following item further emphasizes these criticisms and presents one of the strongest cases against the old subspecies concept.

6. *Geographic variation shows apparent universal non-concordance of characters. Any set of infraspecific categories is a special case, hence accumulated data cannot be used to predict the behavior of un-*

studied characters (Wilson and Brown, 1953; Brown and Wilson, 1954). This criticism of the subspecies concept concerns character correlation (or lack of it) between two or more populations. Character correlation is a measurement of the degree of association between morphological, or other, features throughout the geographic range of a species. It is unfortunate that two terms referring to character correlation, "concordance" and "non-concordance", were originally used in a restricted sense. This dichotomy suggests that there are only two possible conditions regarding correlation between characters, when actually the degree of correlation can assume any value from absolutely none to complete correlation, i.e., a "correlation coefficient" of 0 to 1, or –1. By implication and usage, "concordance" would designate complete character association and "non-concordance" or "discordance," something less than perfect correlation. It is, however, difficult to surmise if this was the original intent, because no precise definition was given. The inexactness of the terms causes them to be of questionable value, but if they were related to a correlation coefficient, they might prove very useful supplementary terms. Of course, "character correlation" is available, as a term, and has the desired connotation.

Brown and Wilson directed their discussions of character correlation toward a refutation of the "subspecies." It must be admitted that, because their remarks were based upon the discussions of taxonomists advocating a loose subspecies concept, their criticism was a valid one. Because of unlike rates in the fixation of different genes throughout a continuously distributed species inhabiting a vast area, it is not likely that complete concordance of genes would ever exist. In fact, in a *continuously* distributed cline (level III) one would expect the exact opposite, namely a number of characters showing independent patterns of variation. (True character concordance in such cases would likely be limited to closely linked genes or pleiotropic effects of a single gene).

Brown and Wilson went on to emphasize why *many* of the old subspecies have no real meaning. The data of Brown and Wilson (1954), Christiansen (1958), Gillham (1956), and Hagmeier (1958) indicate that patterns of clinal variation are usually independent for each character when physical isolation is incomplete or nonexistent. Therefore, naming these demes (level III) as subspecies, results in taxa whose distribution and diagnosis have no reality if new clinal characters are studied.

Edwards (1956a) briefly indicated why *complete* character correlation, i.e., concordance, is *not* to be expected in any deme and why it has little to do with the validity of the "subspecies" as herein defined. However, in completely isolated, well differentiated subspecies (level V) discordance will be of minor significance. In fact, if discordance exists in isolated demes, it is probably the result of very recent isolation (level IV) or parallel evolution of characters (occurring in levels IV or V) in scattered parts of the species range.

7. *Artificial, quantitative methods of separating subspecies are invalid* (Wilson and Brown, 1953). Although artificial, seemingly unnatural, quantitative standards are necessary for a dividing line to delimit subspecies (here the 84 percent rule), they are not invalid. This criticism only emphasizes our inability to measure exactly a particular phenomenon—it does not invalidate the "restricted" subspecies, or any other, for that matter.

Without artificial, perhaps even subjective, quantitative criteria much scientific theory would never have developed. In biology, genetics is a striking example of the successful use of these methods. It is common practice and necessary in science to categorize continuous phenomena into either-or categories. The justification of such procedures on the basis of clarifying relationships and providing useful terms seems reasonable, especially if various dividing points are of additional significance

as they are in the delimitation of "potential incipient species." It is on this basis that the present 84 percent lower limit is reconciled with the new restricted subspecies concept.

8. *Many species are polytypic* (Wilson and Brown, 1953). Using this as a basis for rejecting the *entire* subspecies concept hardly seems justified. There is no recognizable conflict between isolated populations that have independently acquired fixation of the same mutant genes and the subspecies as herein recognized. Polytypic races would not meet the necessary requirement of "a number of obviously different characters."

9. *Insular "races" are incompletely analyzed—they could be either species or subspecies* (Wilson and Brown, 1953). This is no easy problem to solve. However, it is no unique difficulty—previous usage causes it to be a frequent consideration. This means that the systematist will have to become very familiar with the ecology, ethology, physiology, and morphology of the animals he is studying. Therefore, the highest calibre work now being done (this includes biological studies) should be incorporated in critical methods. Although techniques for character analysis are discussed in this paper, these procedures cannot by themselves differentiate between species and subspecies. However, this does not invalidate the "ultimate truth" that insular populations are either species or subspecies (Edwards, 1954, p. 10).

10. *A vernacular locality name can designate a variant just as well as a trinomen* (Wilson and Brown, 1953). Fennah (1955) indicates the confusion that can result from using geographic names to designate populations or groups of populations. Also, such a practice would not differentiate between potential incipient species and lower levels of insignificant divergence. The existence of such levels, even if I have not accurately designated all of them, seems to be supported by existing data. Perhaps some means other than the use of trinominals would be just as satisfactory for designating potential incipient species, but it seems that the high level of divergence required by the "restricted" subspecies definition warrants more permanent nomenclatorial recognition. This premise is based on recognized genetic disjunction, following physical isolation, and upon the resultant high correlation of divergent characters.

This discussion does not suggest a correction for the shortcomings of locality data. Although Fennah's points are well taken, there seems to be no reason for ignoring geographic location even for levels of divergence below the restricted subspecies. Some means of alleviating the confusion of geographic names are suggested by Riemer (1954) in his outline of precise collecting data. However, it does seem that any level can be referred to by morphological, ecological, behavioral, and physiological definitive features, used in conjunction with locality, physiographic province, or biogeographic region reference.

11. *The concept of the polytypic species is typological* (Brown and Wilson, 1954). W. J. Brown (1959) emphasizes that this criticism would be limited to the unrestricted subspecies, and in that respect it might be valid. The theoretical basis for broad "subspecies" recognition is so loose that in practice any studied population might be named because of some character divergence from known populations. Because the primary emphasis in describing the "old subspecies" is character divergence rather than biological relationships, these unrestricted demes might very often be merely typological, as charged. The restricted subspecies, however, certainly does not deserve this criticism because the important criteria are the character correlations developed during physical isolation.

12. *Using geographic isolation to define subspecies is arbitrary. Moreover, there is a definite problem in determining the reality of geographic isolation* (Brown and Wilson, 1954). The acceptability of arbitrary criteria was considered. However,

how can the extent of extrinsic isolation be considered as purely arbitrary if it is the causal factor that eventually allows the isolated demes to differentiate genetically until they display concordance in a number of characters, each segregated from characters of the rest of the species by an 84 percent rule? The second portion of the criticism is not likely to prove an important consideration. Isolation should be suspected whenever sharp character disjunction or habitat disjunction is found, but if there is any real doubt that isolation occurs in a given instance, the isolates should *not* be described as different subspecies in the proposed restricted sense.

13. *Temporal and ecological subspecies probably do not exist* (W. L. Brown, 1957). Brown, although directing his criticism to Edwards' (1956b) use of the terms "extrinsic" and "intrinsic" in discussing isolation of subspecies, implies the above criticism. His criticism of these terms has no direct bearing on the subject of this paper. As a side issue Brown states, "It is impossible for me to conceive of two sympatric populations of a single species that are normally prevented from interbreeding by a separation of their breeding times." Brown also implies that ecologically separated sympatric subspecies (i.e., macrogeographically sympatric, but microgeographically allopatric) are unlikely, but there are a number of studies available that certainly indicate the existence of these.

There are well known examples of possible temporal subspecies. Many butterflies have spring and fall broods that are morphologically distinct, as well as temporally distinct, from one another (there are no broods in between because of weather conditions). Sympatric 13– and 17–year cicadas have no possibility of interbreeding because of gaps of several years when neither occur. Seemingly allopatric *Recurvaria* moths in the Sierra Nevada Mountains of California show temporal isolates; one in Tuolumne Meadows, Yosemite National Park, emerges as adults only during odd years, the other in Mono County, emerges only during even years. Because both have two-year larval cycles, they show complete temporal, and possibly geographic, isolation. As a generalization, there seem to be many examples of "temporal subspecies" among invertebrates and there might be some in vertebrates, possibly fishes, of both sympatric and allopatric temporal subspecies.

There are many examples of ecological subspecies in viruses, bacteria, rickettsiae, and parasitic Protozoa.

Smith and White (1956) have many pertinent remarks concerning why the former definition of subspecies, if used in a somewhat limited sense, should remain acceptable. However, their lack of serious restriction would still allow many criticisms of the "subspecies" to be valid. For example, many very heterogeneous phenomena, as here represented by different levels of infraspecific divergence, could be considered as legitimate subspecies.

Various suggestions by many authors have resulted from the criticisms cited in the present article. For comparative purposes they are summarized in five statements as follows:

1. *Retain the subspecies concept and use of the trinomen in the broad sense defined by Mayr* (Bogert, 1954; Parkes, 1955).

2. *Keep well defined subspecies, as such, but drop the trinomen* (Gosline, 1954).

3. *Keep only step clines and probably divergent, isolated populations as subspecies and use the trinomen* (Hubbell, 1954). Smith and White (1956) also seem to adhere to this position.

4. *Recognize only divergent, completely isolated demes as subspecies, to which the trinomen could be applied* (Edwards, 1954; Van Son, 1955). *Incompletely isolated demes would be considered according to their levels of divergence* (using present terminology), *and, if named, would only be called "morphs," without*

"official" taxonomic priority (Edwards, 1954).

5. *Eliminate the subspecies concept and trinomen entirely. Describe individual character distribution and use vernacular locality designations for particular variants* (Wilson and Brown, 1953).

Methods of Analysis

This section contains a great deal of criticism of prevailing systematic methods. Although procedures are proposed to minimize shortcomings in current practices, no simple solution is (or can be) given. The requirements of these proposed methods are for many forms extremely difficult (perhaps impossible in some cases) to fulfill at the present time. Yet, if systematic conclusions are to be reliable and withstand critical appraisal, few shortcuts are possible—the present proposals are the minimum required for the necessary high standard of taxonomic work. Perhaps recognition of the shortcomings in methodology is the reason for references to systematics "being an art" and for the deference rendered the "taxonomic sense" of certain workers. The methods here proposed seem a minimum replacement for an undeveloped taxonomic sense.

Although many of Brown's and Wilson's views are questioned, these men performed a service in attacking methods and procedures that are far from being the best available. Censure of two generally accepted practices, dating from Linnean times, is a natural outgrowth of their discussions. These practices still occur because advances in "sampling theory" and the "design of experiments" were not incorporated in most methods. This is an unfortunate but understandable result because many systematists do not have a sufficient background in statistical methods. Discussion of these two aspects precedes the presentation of steps for as precise an analysis as seems practical at present.

First, many systematic procedures for designating new species, or subspecies, do not satisfy even the preliminary "steps" of the "scientific method." As a matter of fact, most proposals of taxa below the genus are little more than hypotheses. Surely, the first examinations of specimens (often the only basis for naming new species, or subspecies) does not provide all the intermediate steps between hypothesis and first generalization. Hypotheses certainly have a definite place in systematics as do preliminary ideas in any field. However, it does not seem that the final product of a science should be so largely confined to such low levels of knowledge. At the very least, some test of preliminary ideas appears necessary, and the most direct and simplest approach involves statistical methods. However, any approach should necessitate the study of living specimens in the field and the collection of additional material, before we can bridge the gap between hypothesis and final interpretation of population relationships. Only after acquiring this added knowledge can we arrive at valid conclusions *objectively* rather than *subjectively.*

Finally, it seems that the burden of "proof" is often in the wrong place. Many species and subspecies, diagnosed from a very few specimens, are biologically unknown. Yet, such unknown quantities are "officially" named, and must therefore be accepted without question. If another worker cares to challenge the new taxon, a few specimens, or biological observations, will not suffice. Here, it seems for the first time, detailed study is demanded. When the new taxon is difficult to collect, it might stand simply because revisers cannot obtain sufficient data to question the status of the form. Naming the organism in such cases gives an impression of knowledge that does not exist. In cases where detailed studies would synonymize briefly considered, but rashly named taxons, there appears to be little justification for erection of the original names. Moreover, invalidating such hypo-

thetical names would probably be the only way of encouraging detailed preliminary studies to become commonplace prior to establishing new species or subspecies names.

Although the methods to be developed here below are restricted to infraspecific categories, some mention about distinction between species and subspecies seems in order. This is especially necessary since the proposed subspecies level will often be difficult to distinguish from the species level. The fact that the "restricted" subspecies so closely approaches certain weakly defined "species" makes this situation a reality, but should not be considered a hindrance. The two entities are very close in nature, and that closeness will naturally be reflected in their taxonomy. The only solution might be to make a detailed study of the biology of questionable populations. Admittedly this is not easy; however, it has been done, e.g., the work of Zweifel (1955) showing that two frogs of the genus *Rana, boylei* and *muscosa,* are species. Each group of organisms will provide unique problems in this matter. Some indication of this is given by W. J. Brown (1959), Kincaid (1957), and Camin and Ehrlich (1958).

The following method of analysis considers the problems currently encountered in systematic procedures. Unlike most previous approaches, it provides conclusions from tests of hypotheses and experimental designs based on knowledge of levels of infraspecific variation. Also, it seems to be the simplest, yet scientifically sufficiently accurate, method. The actual statistical methods were chosen for their simplicity so that statistically uninitiated systematists can become more thoroughly familiar with the analysis. A statistician could provide more exacting methods; but, if the methods and results are not perfectly clear to the student of speciation, the biological significance of the statistical results might be lost. Also, these simple procedures can be used by systematists not having the services of a statistician. It might be well to indicate that although these methods tend to make the use of a mechanical calculator necessary, they are still considered very simple.

The recommended procedures for infraspecific analysis can be reduced to a few steps. These are as follows:

1. *Select a problem suitable for study.* At the present time it is common practice to "name" essentially unknown quantities. If investigations are to be of the desirable high order, this situation must be changed. Without certain knowledge available, there is really no basis for more than an opinion about the status of any demes. The primary need is for specimens that adequately encompass the distribution of the animals to be studied.

Museum specimens can be used for a tentative hypothesis about the animal's infraspecific relationships. This can be accomplished by simply mapping sample means, and then isophenes, for each of many characters. Four main benefits result from such data. *First,* characters will be found that can be considered for preliminary study. *Second,* orderly trends in characters may suggest that conventional collecting procedures result in samples not significantly different from random samples (Pimentel, 1958). This can be tested (Dixon and Massey, 1957, sec. 17–12). *Third,* critical geographic areas, seasons, and habitats will be suggested, as will critical rates of morphological change. These will suggest the number and placement of the grid of localities for final analysis. *Finally,* the museum data plus the method of Cochran and Cox (1957, sec. 2.2) will aid in determining ideal sample size for the "preliminary study" discussed below. This method might well be repeated when the preliminary study data become available, thereby obtaining more accurate sample size for the final analysis.

2. *Make a preliminary study of the species.* This procedure has been previously outlined in some detail (Pimentel, 1958). In a preliminary study valid features can be selected for study and further bases for

hypothesis about the patterns of variation within the species may be established.

The variation pattern hypothesis provided by museum specimens may or may not be altered by the preliminary study. In fact, museum specimens, preliminary study specimens, and final analysis specimens may each indicate some difference in the general patterns of variation. If this occurs reliance must be placed on the results of the final synthesis and analysis. The nature of the methods are such that only the final analysis has great reliability. However, if marked differences occur in these three groups of data there may be some reason to question the final results. In practice the first two analyses will probably barely indicate a pattern of variation and the final analysis, depending upon the number of localities and specimens from each locality, will delimit critical areas in the pattern, e.g., location of steps in a step cline and any other areas of homogeneity or disjunction in a character.

3. *Select the localities for final analysis.* These localities should be as nearly equidistant from one another as is possible. The maximum permissible distance between localities can be determined from the results of steps one and two. Two things must be kept in mind when choosing this distance. First, localities too close together will not show much difference in animal morphology, etc., but localities too far apart will display such large differences as to obscure the pattern of variation within the species as a whole. Only the latter consideration is a problem. The former situation indicates that unnecessary work was done. *Second,* the more localities used, the greater is the precision of the statistical analysis. The primary consideration then is that too few localities might be used so the trends that exist are likely to be obscured.

4. *Choose the sample size and collect specimens.* The "proper" sample size depends upon the number of localities and the amount of variation between and within localities. The method of analysis considers patterns of variation, i.e., which localities show the same and which show different characters; but it does not show quantitative change from collecting site to collecting site. Although amount of change could be estimated, it would be of little practical use because we are limiting the study to diagnosing patterns, emphasizing areas of homogeneity and determining breaks in (clinal) variation of individual characters.

The important consideration for samples are (1) that they must be random samples, and (2) that they be as large as possible or practical. The consequences of too small a sample size is the same as for too few localities—the two are directly associated in this respect. Because of sample size-locality association one can use smaller samples and more localities. The converse is not true—it might obscure the pattern of variation.

5. *Analyze the accumulated data.* Many variable characters should be studied. Simultaneous analysis of all characters is possible, but very complex. Such analyses involve codification of data on cards and use of a computer. Although this is the ideal procedure, analysis of a large number of characters individually is entirely satisfactory. Isophenes resulting from each individual character analysis should be mapped on a distribution graph. It might be necessary to use more than one graph for clarity. In any event, the end result would be a pictorial representation of character correlation (i.e., concordance or discordance) and levels of divergence.

Analysis would be made by Factorial Design, a kind of Analysis of Variance.[1]

[1] The term "Analysis of Variance" is frequently restricted to single factor considerations, e.g., differences between localities; "Factorial Designs," indicate two or more ways of classification, e.g., comparing both sexes and localities. Analysis of Variance, however, also refers to the entire range of procedures involving a particular group of statistical methods and therefore can include both single and multiple classifications.

The Factorial Design involved in most instances might be a "two-way classification with equal number of observations per subclass," the two classifications being (1) sex and (2) localities. If neither sexual dimorphism, nor any other factor is involved (Pimentel, 1958), a single classification (i.e., localities) Analysis of Variance would be used. For the Analysis of Variance, including Factorial Designs, all samples from all localities *must* be of the same size.

A brief outline of possible procedures follows:

a. The first test is an Analysis of Variance or Factorial Design. Computations for single classification (Li, 1957, sec. 12.3) or two-way classification (Li, op. cit., sec. 18.4) are made.

b. If any treatment, e.g., locality or sex is found statistically significant, the next procedure is to make a series of Trend Tests, using orthogonal polynomials.[2] Trend Tests are here so called because they indicate the trend of the data (i.e., the pattern of character variation). The simplest or first order Trend Test is the Linearity Test—progressively higher order Tests are the Cubic, Quadratic, etc. These tests are *not* made under any other circumstances than a "significant" Analysis of Variance. Although each of these Tests involves a number of steps, they are fairly simple to accomplish. For example, if localities are found to be "significant," the following computations are made for each Trend Test. In the first group of "steps," computations involve individual manipulation of the data from each separate locality—at *no* time are figures from one locality involved with any other locality. The steps are as follows: (1) obtain individual sums of the measurements for each locality; (2) square each locality sum; (3) divide each squared figure by the number of individuals (i.e., measurements) in each locality sample—because all samples should be of the same number of organisms the same divisor will be used on each squared total; (4) multiply each resultant figure by the appropriate coefficient of the proper orthogonal polynomial (unlike orthogonal polynomials, hence coefficients, constitute the only difference among Trend Tests); and (5) divide each total by a common divisor (obtained from the sum of the squares of all orthogonal polynomial coefficients of that particular Trend Test). The final two tests then consist of (6) summing all results obtained in step 5; and (7) tabulating the result as a "mean square" in the Analysis of Variance table with one degree of freedom.

If the Linearity Mean Square is the only Trend Mean Square that is "significant," it follows that the character under consideration follows a graded cline.

c. Further tests are made *only* if a Trend Test other than or in addition to the Linearity Test is "significant," i.e., the data do *not* imply a graded cline. To summarize previous steps, if the Analysis of Variance indicates locality "significance," this means that characters are not homogeneous and some pattern of variation is found in the species. In the Trend Tests if *only* the Linearity Test is "significant," this means that the pattern of character variation follows a gradual cline. However, if any Higher Order Trend Test is significant, it is likely that the pattern of variation follows either a step cline or some irregular pattern.

To determine the exact distribution of character disjunctions, another test must be made. The best test for diagnosing these more complex levels is the Multiple

[2] The theoretical aspects of orthogonal polynomials are considered by Fisher (1950, sec. 27), an example of their use is given by Snedecor (1946, sec. 15.6), and a Table of Coefficients is given by Fisher and Yates (1949, Table XIII). As Cochran and Cox (1957, sec. 3.42) indicate, these Trend Tests do not require equal sample sizes. However, the general Analysis of Variance, including Factorial Designs, and the Trend Tests are much more complex to calculate, and further tests (step "c"), are *not* possible if unequal sample sizes are used.

Range Test. Li (1957) gives a detailed, simple discussion of the steps in calculation. Here it is sufficient to reemphasize that the test groups together localized samples showing insignificant differences from one another and separates those with "homogeneous" characters from similar groups whose characters are "significantly" different.

d. The final step is graphing results on a range map of the species. This involves no more than plotting lines of equal, or similar, phenotype (i.e., isophenes). In the case of a graded cline (indicated by a "significant" Linearity Test and no Higher Order Test "significance"), equidistant isophenes would be drawn on the distribution map. Because of the linear character gradient any convenient number of isophenes, as long as they are equidistant from one another and of sufficient number to portray a graded cline, can be used. In the case of step clines or irregular patterns (indicated by a "significant" Multiple Range Test) isophenes are drawn around homogeneous groups.

6. *Diagnosis of Levels.* After all analyses are made and isophenes graphed, levels of divergence can easily be read from the graphs. These graphs would have two advantages over conventional presentation of data. *First,* they would emphasize relationships within the species as a whole. *Second,* they would allow other workers to make their own interpretation of the results.

Levels of divergence would be diagnosed from graphs as follows: *Level I:* collecting data, as plotted, indicate continuous distribution of the species and no "significant" differences in any characters among populations. *Level II:* data indicate discontinuous distribution within the species and no differences in characters among populations. *Level III:* continuously distributed species with (*IIIa*) graded clinal, (*IIIb*) step clinal, (*IIIc*) irregular, or (*IIId*) combinations of clinal and irregular patterns. *Level IV:* discontinuously distributed species with (*IVa*) graded clinal, (*IVb*) step clinal, (*IVc*) irregular, or (*IVd*) combinations of clinal and irregular patterns. *Level V:* the restricted subspecies, consisting of physically isolated units within a species, *if* these units show consistent and "significant" deviations from the general pattern of species variation as measured by the 84 percent rule (Pimentel, 1958). It will be noted that an additional sublevel has been created in Levels III and IV.

Certain descriptive terms might be of use in referring to a particular level or population within a level. *Only* the physically isolated subspecies (level V) would be referred to by a trinominal designation. All "valid" trinominals would, therefore, be "official" and automatically indicate the restricted subspecies. Any subpopulation within a restricted subspecies could also be considered by its particular level of divergence as found *within* the subspecies. Species displaying discontinuously distributed clinal and/or irregular patterns (level IV) could have each "distinct," isolated deme represented by the term isolate. An *isolate* is a deme that is allopatric (physically isolated geographically, ecologically and temporally) in relation to adjacent demes and is recognizably different (morphologically, physiologically and/or ethologically) from other demes of its species, *but* not to the extent of 84 percent rule divergence *in a number of characters.* Isolates might be named on the basis of a geographical, physiographic, or biogeographical designation; perhaps an ecological, temporal, physiological, or behavioral reference, if it clarifies the description; and the word "isolate" (e.g., Sierran swamp isolate, indicating location in the Sierra Nevada Mountains of California and the significance of a swamp habitat). Edwards (1954) has already provided a term, *morph,* for "distinct" units of continuously distributed species displaying clinal and/or irregular variation patterns (level III). A *morph* is a deme that is sympatric (geographically, ecologically, and temporally) with adjacent demes of

its species and is recognizably distinct in certain features (morphological, ethological, and/or physiological). One might also consider as morphs such demes within a level V subspecies. Naming of morphs could be on the same basis as that for isolates, the only difference being the substitution of the word "morph" for the word "isolate." It is *not* believed that patronyms would serve any useful purpose in describing either isolates or morphs. Levels I and II do not seem to require any special term of reference. These demes can be linked with biogeographical, etc. reference and referred to as being either allopatric (level II) or sympatric (level I), e.g., sympatric Sierran deme, or allopatric Sierran deme. These usages might be better understood than would be constant discussion of either levels or sublevels. Sublevels, of course, could be designated by the already existing terms that describe these patterns of variation.

7. *Final Interpretation.* Certain aspects of the analysis need further emphasis.

The statements concerning the Analysis of Variance in an earlier paper (Pimentel, 1958), for example, indicate items that should be clearly understood by anyone using these statistical methods. The recommended references, especially Li (1957), emphasize these items.

Second are the factors that effect the precision of the analysis, and what "control" systematists have over these factors. The ability of the "experimental design," i.e., the above calculations, etc., to emphasize differences is directly related to sample size and number of suitable localities utilized for the final study. The greater the magnitude of either, or both, the more true interlocality differences will be discovered. Therefore, if too few localities are represented, or if too small a sample size is studied, differences that exist in nature might not be discovered by the analysis. This might cause undue concern about the adequacy of the final analysis in some cases. *If* the preliminary study includes at least one sample from each extreme and one from the center of the animal's range (more samples are preferred) and *if* they are "significantly different" from one another, samples from each locality (*if* each conforms to the preliminary survey samples) should reveal additional differences, if they actually do exist. Of course, this is true only if the differences indicated by the preliminary study were *not* due to chance or nonrandom sampling.

Third, the statistical and graphic analyses tend to emphasize relationships rather than differences. This can be appreciated better if the reader becomes more familiar with some of the statistical tests made only when the Analysis of Variance shows "significant differences" among localities.

Fourth, contradictory results can be obtained from the Multiple Range Test. If a difference is revealed among local populations by the Analysis of Variance and Trend Tests in addition to or other than the Linearity Test, this indicates step clinal or irregular variation and the Multiple Range Test is then used to determine the more exact nature of the variation. If character disjunction is slight and (especially) if too few localities and/or too small sample sizes are used, conflicting Multiple Range Test conclusions might even result. For example, if localities A, B, C, D, and E represent sites on a step cline, the MRT might give results as follows:

A is "significantly" different from C, D, and E, but not B; and B is different from D and E, but not A and C. Moreover, C is different from A, but not D and E. This would imply in one test that A shows the same variation as C, but in the other test that they are "significantly" different. The above data indicate two "homogeneous parts" in a step cline, namely A and C-D-E, plus a sample from the intergrade area (namely B). Therefore, even when character "breaks," sample size, and localities are not large enough for clear disjunctions to be indicated by the Multiple

Range Test, patterns of individual character variation can often be intelligently diagnosed.

Summary

Various degrees or levels of divergence are recognized within species. During recent times, representatives of nearly all of these levels have been described as "subspecies." Consequently, much dissatisfaction with the subspecies concept has been expressed. This dissatisfaction has resulted in suggestions either to restrict or eliminate the concept and the latinized trinomen. However, the trinomen does serve a definite purpose if it is restricted to populations that are "potential incipient species." Such "restricted" subspecies can be accurately delimited only after a thorough study of the variation within the entire species; the practice of naming subspecies without considering their genetic relationships does *not* contribute significantly to knowledge concerning the speciation process.

Five levels of infraspecific divergence are proposed and graphically illustrated: (1) continuously distributed homogeneous species with uniform infraspecific variation; (2) discontinuously distributed homogeneous species with uniform infraspecific variation; (3) continuously distributed species with (3a) graded clinal, (3b) step clinal, (3c) irregular, or (3d) combinations of clinal and irregular patterns; (4) discontinuously distributed species with (4a) graded clinal, (4b) step clinal, (4c) irregular, or (4d) combinations of clinal and irregular patterns; and (5) the subspecies, as restricted in this article. This proposed level of subspecies discrimination is essentially the same as that proposed by J. Gordon Edwards in the pages of this journal and elsewhere. The fifth level subspecies is a physically isolated, obviously different entity that would crossbreed with the rest of its species IF contact occurred under natural conditions. For purposes of greater precision in determining *how different* the physically isolated entities must be in order to merit subspecific designation, it is here proposed that several characters must show *consistent* deviations *as measured by the 84 percent rule* (Pimentel, 1958), i.e., complete character correlation (concordance) to this extent.

These five levels are differentiated by the two primary factors of speciation, namely physical isolation and the resultant genetic divergence. The levels are limited to five in number because it is doubted that additional distinctive levels could readily be distinguished in nature. It is believed that the levels are justified on the basis that various heterogeneous phenomena, all of which are called "subspecies," occur in nature and that some attempt should be made to distinguish, or differentiate, among these phenomena. Moreover, the establishment of such recognizable levels will eliminate the extremely subjective practice of considering "subspecies" as being whatever any self-adjudged "competent" systematist believes worthy of description as such, with an indestructable latinized trinomen. Also, the use of these levels allows the application of a standardized analysis of infraspecific variation and a more precise definition of the subspecies category. Criticisms of the broad, neo-Darwinian subspecies are considered in light of the new restricted subspecies concept.

Severe criticism is directed toward present, unreliable methods of infraspecific analysis, and reliable procedures are proposed and outlined. These procedures include the Analysis of Variance, Trend Tests, Multiple Range Test, and a test that will assure a minimum of 84 percent character divergence in physically isolated, divergent populations, thereby giving greater precision to the proposed restricted subspecies definition.

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Mode of Life, Functional Morphology, and the Classification of Modern Teleostean Fishes

WILLIAM A. GOSLINE

THE classification of modern teleostean fishes has been constructed empirically. The result has been called by Garstang (1931: 240) "a proliferation of pigeon holes." Pigeonholing certainly serves a useful purpose, at least in the preliminary phases of classification. Nevertheless, the present author would hold with Sylvester-Bradley (1956: 3) that "taxonomy is primarily a study of relationships." The obvious way to determine the relationship of modern forms is to trace their genealogies back through the fossil record. But for modern teleostean groups the crucial fossil evidence is almost always lacking, at least as yet. The only alternative is to construct hypothetical genealogies. It is the thesis of the present paper that some effort to understand why living forms are as they are can aid in hypothesizing the routes over which they came.

If this thesis is accepted, it no longer suffices to determine whether a character is present or absent; rather, one must ask in addition: "What does the character (or its absence) mean to the animal?" However, the answer to such a question can rarely be given in terms of individual structures, because changes in structure are usually of importance only insofar as they change the selective value of the integrated system of which they form a part. It is the functional system that runs the gauntlet of selection and that evolves, and therefore it is the system as a whole that is of primary concern for the student of phylogenetic histories. Now the system may evolve in response to continuous selection of a uniform type, or the nature of the selection pressure may change. Such a change occurs, for certain systems at least, when the fish adopts a different mode of life. The rest of the paper will discuss examples of the interrelationship between mode of life, functional anatomy, and the classification of modern teleostean fishes. These examples are ones with which the author is acquainted at first hand. (Many of them draw upon data presented in his systematic papers.) Others equally good or perhaps better could have been taken from such works as those of Günther and Deckert (1959, etc.), Makushok (1958), etc., etc.

Simpson (1944: 206, 207) has stated that the majority of higher taxonomic units have evolved through "the rise of a distinctively new adaptive type." Among fishes it is easy to think of major teleostean groups that conform to Simpson's postulate. The remoras with their dorsal suckers by means of which they ride along on larger animals and the angler fishes with their elaborate fishing pole methods of capturing food at once come to mind. However, I would like to use as an example here the eels. The eels constitute one of the best differentiated groups of modern fishes. Yet all their peculiarities seem attributable to the one basic habit of wedging themselves through small holes in the coral or rocks. The body shape is the most conspicuous, though by no means the most distinctive, modification for this mode of life. The heavy skin, with the

reduction or complete loss of scales, the invariable absence of pelvic fins, and the frequent reduction or loss of other fins in modern eels are further features of the same type. Far more distinctive, however, is the skeleton of the head region. In the head there has been considerable fusion of elements especially at the forward end, e.g., the fused premaxillary-ethmovomerine block, and a reduction or loss of superficial covering bones, e.g., circumorbitals and opercular bones. The general result is that the eel skull has become consolidated and simplified into a pipe-like structure. Eels frequently use their head as a wedge to pry open sufficient space for the body to pass through. It is a common sight in the Tropical Pacific to see morays forcing their way under rocks or even under the shoe one is standing in. Numerous other eel characters that would seem to be adaptations to this same mode of life could be cited, but two further examples from the respiratory and sensory systems will suffice here. As to sensory systems, the eels have undoubtedly the largest olfactory surface relative to body size of any fishes, and their sense of smell is notorious. On the other hand their eyes are usually small and their sight poor (Bardach, Winn, and Menzel, 1959). With regard to respiration, the eels are again highly distinctive. Normal fishes force water across the gill surfaces in part by expanding and contracting the gill covers. In eels the gill covers are greatly reduced and water is forced over the gills by pumping it back through the gullet; to make such a swallowing system effective the mouth and the gill chambers must be separated by a considerable interspace. To this end, the gills have not only been displaced backwards, but the pectoral girdles have been carried back with them and lose their usual articulation with the fish skull.

In these modifications of the head region the eels have progressed far beyond the other groups of fishes with an eel-shaped body, e.g., carapids or symbranchids. In making not one or two but a whole series of adjustments to a particular mode of life the eels have evolved into a very successful group of animals. (In Hawaii, for example, the morays are the second largest family of fishes, so far as number of species is concerned.)

There are two points about this success that deserve discussion. One is that it *per se* discourages evolution of other groups in the same direction. Were it not for the presence of a well-adapted eel in every nook and cranny of the tropical reef other fishes would have undoubtedly evolved further in an eel-like direction, and the distinctiveness of eel structure would have been blurred. (Perhaps there is something of a who-got-there-first principle in evolution.) Second, the harmonious combination of functional systems in eels would appear to have permitted them to penetrate other environments than that in which they seem first to have evolved. The transition from a crevice-haunting to a burrowing existence is the most obvious possibility. Indeed, around Hawaii the eels form by far the largest single group of burrowing fishes. Less expected perhaps is the fact that several eel families have successfully taken up a bathypelagic mode of existence.

Many modern teleostean groups resemble the eels in having adapted themselves to some more or less specialized mode of life. However, among living fishes are also forms which are close to or represent points along a sort of base line of teleostean evolution. Such a line would seem to run very close to the clupeiform (isospondylous) genus *Elops*, thence to the scopeliform (iniomous) *Aulopus*, from there to the vicinity of the berycoid *Polymixia*, and finally to the percoid *Epinephelus*. Now all the four genera mentioned are tropical or subtropical, marine, bottom-living (*Elops?*), generalized carnivores. There appears, in short, to be no major change in adult mode of life from the bottom to the top of the series, though minor changes are of course present.

In this base-line sequence, the struc-

tural changes that do occur have nothing like the magnitude of those found in the more specialized groups, e.g., the eels. Nevertheless evolutionary advances have taken place. It would seem that many at least of these advances are not the result of adaptation to changed modes of existence.[1] Rather, they would appear to be generalized improvements that have as a main prerequisite for their appearance a particular level of structural organization. Thus, in the series given *Polymixia* and *Epinephelus,* like most higher teleosts, have a protrusile upper jaw; *Elops* and *Aulopus* do not. In most, though by no means all, occasions a protrusile upper jaw would seem to be advantageous in feeding. Indeed, protrusile upper jaws of different types have been developed in various groups far below the *Polymixia* level of teleostean evolution. Presumably these divergent types have either been too specialized or have developed in fishes that were in other ways too specialized to "take" in more than the particular group.

To get back to the base series, the berycoid-percoid type of protrusile jaw could not apparently have developed directly from *Elops* because of inappropriate ligamentous attachments. These in turn seem to be related to the fact that in *Elops* the maxillary forms part of the upper jaw. However, in *Aulopus* the maxillary has become excluded from the gape and the ligamentous attachments of the jaws are about as in the berycoids and percoids. In short condition A must be followed by step B (and possibly B_1, B_2, etc.) before C can occur.

My second example deals with the loss of a bone. The orbitosphenoid is found in most lower teleosts through *Polymixia* but is lost in *Epinephelus* and all higher forms. Though the presence of this bone runs well up in the base line of the lower teleosts it drops out in many of the side lines. Indeed in all those lower teleosts that, for whatever reason, retain a larger amount of cartilage than usual in the cranium, the orbitosphenoid disappears.

My last example concerns the caudal structure. The tail of a fish is the chief organ of forward motion and as such is of considerable importance to the fish. The history of how a heterocercal tail, such as that found in most sharks, has evolved into the symmetrical structure found in the teleosts is frequently told. The account is usually given in connection with embryonic recapitulation. Here I would like to discuss aspects of the same story from the viewpoint of adult functional morphology. We may start with the fact that the most efficient shape of tail for rapid forward locomotion is the forked type (Gero, 1952). This tail shape is very old, antedating the teleosts and almost attained, for that matter, in certain sharks, e.g., *Carcharodon.* It is found in *Elops, Aulopus, Polymixia* as in most modern teleosts. Functionally the two most important rays in such a tail are the ones that border it above and below; these form cutwaters and limits as it were to the fin. Now in a fork-tailed fish the number of principal rays is usually quite constant, 19 in most lower teleosts, and 17 in most higher forms. There are also diverse groups of round-tailed fishes. In these however, the number of principal rays often becomes highly variable, presumably because the restricting limits have disappeared.

As to the supporting skeleton of the caudal fin, the functional problem here is to change over a flexible, horizontally aligned mast with sail (heterocercal) type of structure to one in which the rear border of the axial skeleton acts as a vertical hinge. To attach a broad hinge to the tip of an abbreviated mast is not a structurally sound solution. As a compromise, the earliest teleosts have a rather abruptly upturned tip of the vertebral column, to

[1] On the other hand certain differences between *Aulopus* and *Elops* would seem to be related to the fact that the former is more of a bottom-living form than the latter. Perhaps, a slight change in mode of life may trigger these more conservative general advances?

the back of which the edge of the hinge (the anterior part of the hypural fan) is attached.

The transition from an upturned vertebral tip to a symmetrical type of hinge occurs very slowly in the basal series of teleostean evolution. Indeed the caudal skeleton of *Epinephelus* is not much different from that of *Aulopus*. It is only at the very upper end of the main teleostean series that a truly symmetrical caudal skeleton is approached. There are, however, innumerable specialized offshoots, e.g., the pipefishes, many catfishes, cyprinodonts, etc., of far less advanced groups that have developed an internal symmetry. In almost all such instances the fishes are notable for a rounded (or pointed), rather than a forked, caudal fin. It would seem that in such a rounded (or pointed) tail the pressure for retaining the old type of caudal skeleton has been released and that the caudal skeleton has gone on to achieve its symmetrical endpoint with relative rapidity. To put it another way, so long as the forked caudal is maintained the caudal skeleton supporting it can only undergo minor evolutionary steps that do not alter the functional integrity of the whole system, but once the shape of the tail changes the rest of the system is free to undergo more drastic readjustments.[2]

In the above paragraphs an attempt has been made to distinguish two types of evolutionary change in modern teleosts: a relatively rapid type presumably related to changes in mode of life, and a slower, more conservative type apparently associated primarily with level of structural organization. In any fish group different functional systems will ordinarily show the results of the two processes (mosaic evolution). So far as classification is concerned, it will in general presumably be the more radically changed systems that are used for defining the group, but the more conservative ones that indicate its relationships. A rather obvious corollary of this generalization would be that it should prove more difficult to determine the relationships of a group, e.g., the eels, in which a specialized existence had affected a large number of structural systems than one in which the mode of life had affected only a few.

A final point about the conservative type of change perhaps deserves mention. It is generally agreed among ichthyologists that there are relatively "primitive" groups of teleosts, e.g., the Clupeiformes (Isospondyli), and relatively "advanced" groups e.g., the Perciformes (Percomorphi). Because of the custom of emphasizing the distinctive features of groups, it is frequently forgotten that the more advanced members of primitive groups may be at a considerably more "advanced" stage of evolution than the primitive members of advanced groups. Thus, to this author, *Epinephelus* would seem to be a more primitive fish than the herring. In short the members of any one group may run a large portion of the evolutionary gamut of modern teleosts. Now, if the conservative characters are dependent upon structural level of organization, this might explain why the member of the fish group most primitive in one non-modified structural system is frequently the most generalized in others. (The author, in studies on structural systems previously little used in classification, was repeatedly surprised to find how often this proved true.) A final obvious suggestion based on this observation, whatever its cause, is that in working on the evolution of a functional system or on the relationships of a group, one does well to start with that

[2] The fact that some fishes in various groups have developed rounded caudals does not mean that the caudal skeleton has also changed. Indeed *Epinephelus* is a round-tailed fish with a typical fork-tailed supporting skeleton. But it does seem to mean that the selective forces that maintained the functional integrity of the old type caudal skeleton are gone. Presumably once the breakdown in the integrated system of such a caudal skeleton is initiated, the latter would pass to a new adaptive type fairly rapidly (Simpson, 1944).

member of a group that is generally considered to be its most primitive member.

The above points may be brought together somewhat as follows. The main route of teleostean evolution seems to have been relatively conservative, both in regard to structure and to mode of life. The various offshoots of this main route, which mostly represent adaptations to specialized modes of existence, have undergone far more drastic structural changes. Some of these represent the same sort of advance in organization that is attained much farther up along the main route. The explanation for this given here is that a change in mode of life, through a change in selection pressures, permits a rapid breakdown of the integrity of the old structural system and thence a relatively rapid reshaping about some new (and presumably better) functional organization. The main line, without alteration of selection pressures, must do this same reshaping far more gradually, but it often manages to do so none the less; it would seem to have, however, the long-run advantage of not having become specialized for any unorthodox mode of life in the process.

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Points of View

Similarity, Ancestry, and Scientific Principles [1]

Bader (1958) disagrees with my suggestion in an earlier paper (Bigelow, 1958) that one of the basic tenets of the phylogenetic school of taxonomy might not be a valid working principle. The tenet in question is the assumption that similarity corresponds with recency of common ancestry. Bader quite rightly points out that this assumption must be valid in many instances, especially when differences in relative similarity are very great. For example, the probability that any two plants share a more recent common ancestry with one another than with any animal is very high. I know of no one who doubts this. Both Bader and I agree that the assumption is likely to be correct in some, but not by any means in all cases. As Bader, Simpson (1945), and many others have pointed out, it is readily apparent that the most similar organisms must share the most recent common ancestry in a great number of cases. There is no disagreement on this point. On the other hand, parallel evolution and unequal rates of evolution ensure that the most similar organisms will not share the most recent common ancestry in a great number of cases, as Simpson (1945), Romer (1949), Bader and others have also pointed out. Again there is no disagreement. We are left with an assurance that similarity will both correspond and fail to correspond with recency of common ancestry, but without a means of distinguishing between the sheep and the goats. Since we are certain that our flock is contaminated with goats, and have good reason to suspect that the contamination is heavy, we are not justified in stating, *even as a hypothesis,* that our flock is composed entirely of sheep.

We know beyond all reasonable doubt that similarity does not correspond with recency of common ancestry in many cases. Therefore, the bald assumption that it does is not even a valid hypothesis, least of all an axiom or principle. Because Simpson (1945) was aware of exceptions to the assumption that homologous similarity is directly proportional to recency of common ancestry, he was not justified in his claim that this assumption is a "valid working principle." Certainly no such "principle" should be regarded as the very basis of systematics itself.

Bader remarks that "we are not concerned with certainty, or the lack of it, but with the probability that an hypothesis is true." This statement is correct, but we are concerned with the probability that an hypothesis is *true,* not with the number of times it is known to be false. Scientific principles are truths. If it is true that one red ball is present in a bag with a million white balls, it is not true that all the balls in the bag are white. If the presence of the one red ball is unknown, the assumption that all the balls are white will be, after a few drawings from the bag, a valid hypothesis. After many drawings of white balls it might be reasonable to claim that our hypothesis has been verified and that it can now be stated as an axiom or principle that all the balls in the bag are white. We are not concerned with certainty, but with probability, and the probability that all the balls are white is high—until the one red ball is drawn! When this discovery is made the probability that all the balls are white is zero, and our axiom is no longer even a valid hypothesis.

[1] Contribution from the Faculty of Agriculture, McGill University, Macdonald College, Quebec, Canada. Journal Series No. 447.

There are stages during the testing of an hypothesis when it may be difficult to decide whether or not verification requires further tests. The opinions of highly qualified scientists may differ as to the quantity of lunar soil that should be sifted before absence of life on the moon can be verified. Certain scientists may refuse to accept even the most venerable scientific laws, and occasionally such scientists may simultaneously split atoms, laws, and hypotheses asunder. Nevertheless, verification is the act of proving an hypothesis to be true, not an estimation of the number of times it is known to be false. The axiom that atoms were indivisible meant that atoms were indivisible. When the very first atom was split this axiom ceased to be even a valid hypothesis.

It might be stated as an axiom that similarity *often* corresponds with recency of common ancestry, or, as Bader suggests: "that there is a very significant degree of cause-and-effect association between homologous (or, by inference, genetic)[2] similarity and recency of common ancestry." These statements are true, and thus qualify as principles. Their value, however, is doubtful since we do not know how often or to what degree the correspondence exists, and since we cannot distinguish those cases in which it does from those in which it does not. A taxonomist or paleontologist who measures recency of common ancestry by comparing similarity is forced to disregard past rates of evolution, forced to use the assumption in its naked, pristine, unqualified form. His conclusions, therefore, are based on an invalid assumption. He cannot even state the probability that his conclusions are correct with any degree of accuracy. To ignore past rates of evolution in stating the relationship between similarity and recency of common ancestry is like ignoring pressure in stating Boyle's law. Given only similarity, the determination of recency of common ancestry without any means of measuring past rates of evolution is like determining the pressure of a gas from its volume alone, without any knowledge of the temperature in or around the container.

Bader cites frequency of mutation as direct evidence that similarity corresponds with recency of common ancestry. He admits that selection pressures may "vary tremendously" but claims that "their average effect must be approximately the same order of magnitude within most groups most of the time." Even if it were valid, this line of reasoning would merely indicate that the assumption in question cannot always be wrong, which no one denies. Actually, mutation rates may have but little effect on the evolution of organisms that are well adapted to a fairly constant environment. Deleterious mutations will be continually selected against. Sudden changes in environment, however, may effect sudden evolutionary changes far surpassing in speed those possible from mutation rates alone. Such changes may take place in one line but not in others. Tremendous discrepancies between similarity and recency of common ancestry can occur despite universally "constant" mutation rates (e.g., man, mackerel, and *Latimeria*). Although selection pressures may be fairly uniform on the average, "tremendous variation" in some but not in other lines will produce many exceptions to the "principle" in question.

Kiriakoff (1959) claims that what I called the phylogenetic school of taxonomy has nothing to do with phylogeny, being based on *"typology of idealistic morphology."* He himself subscribes to what he calls the *"modern* phylogenetic systematics (not school)" which, he says, "emphatically rejects" the same three assumptions that I suggested the phylogenetic school should reject, namely, (1) that similarity corresponds with recency of common ancestry, (2) that phylogeny can be reconstructed without fossil evidence, and (3) that classification should

[2] Both homologous and genetic similarities are inferred.

be based on conservative rather than on adaptive characters. The very basic principle of this modern phylogenetic systematics, he says, is the assumption that "similarity is not synonymous with blood relationship." He regrets that "modern phylogenetic systematics seems to be quite unknown in the United States."

Kiriakoff does not subscribe to my view (Bigelow, 1956) that if classification is to correspond with evolution it must be based on the overall difference rather than on time. Since time must pass and space must exist before evolution can occur, he concludes that classification must be based on time and space as well as on overall similarity and difference (i.e., "holomorph") if it is to correspond with evolution. He claims that "the degree of common descent must be established using as many characters as possible, these characters being *temporal, spatial,* and *individual.*" He does not, however, explain how this is to be achieved, nor does he define "degree of common descent." If recency of common ancestry is rejected emphatically, and if similarity is not synonymous with "blood relationship," it might be asked how "degree of common descent" can be determined from *either* time *or* similarity. Just what, indeed, is meant by "degree of common descent?"

Although I agree that classification should be based on similarity and difference in as many characters as possible (or on "holomorphs" which include all characters of all developmental stages), I do not see how it can be based on time, space, and holomorph simultaneously. Certainly time and space are important factors in evolution, but they are not in themselves the *results* of evolution. The "holomorphs" alone are the results of evolution, and it is these that must be classified before the many and varied factors that have produced them can be studied and understood. Even in the case of fossils, classification must be based primarily on similarities and differences in the surviving remnants of the holomorphs; only after this has been done can the roles of time and space be studied. It is conceivable that a series of horizontal classifications might be based on time by grouping all Permian fossils, for example, in a single Permian hierarchy, all Triassic fossils in a single Triassic hierarchy, etc., but even here classification within each horizontal hierarchy must be based on similarity and difference. Actually, the age of fossils is generally ignored in contemporary classifications. An animal is placed among the Reptilia, for example, entirely on the basis of its overall similarity to other reptiles, whether it lived in the Permian or the present, in the eastern or western hemisphere, and, incidentally, whether or not it shares a more recent common ancestry with birds than with lizards. It is one thing to base studies of temporal and zoogeographical factors on classification, but quite another to actually base classification itself on these factors. Pre-existing classifications facilitated the formulation of Darwin's theory of evolution. Being based on the results of evolution, these classifications helped to reveal the fact of evolution, even though they were produced by men who believed in special creation. In the same way, classifications based on the results of evolution (i.e., on overall similarity) can facilitate studies of the roles that time and space (and other factors) have played in producing these results, without having been *based* on time and space. Natural selection has also played an important role in evolution, but it is not therefore necessary to *base* classification on natural selection.

Before concluding I would like to correct a misinterpretation of a statement made in one of my previous papers (Bigelow, 1958). Bader says: "Bigelow suggests that, subsequent to the cockroach-grasshopper dichotomy, another line could have arisen from the roaches in the Carboniferous which also became grasshoppers." This is not what I suggested. I said: "Does one existing genus of roaches share a more recent common ancestry with another genus of roaches, or with grasshoppers? Does the German

cockroach share a more recent common ancestry with the American cockroach, or with the praying mantis? Roaches were present, as such, in the Carboniferous. They have changed relatively little since that time; but has there not been sufficient time for one phyletic line, derived from roaches, to become grasshoppers since the Carboniferous? Amphibians have produced men in the same span of time!" I did not mention two discrete lines of roaches, each leading independently to grasshoppers, nor did I suggest that any dichotomy occurred "in" the Carboniferous; I said "since" the Carboniferous.

Bader concludes that parallel evolution and unequal rates of evolution do not invalidate the "generally accepted relationship as a general principle." Kiriakoff concludes that what I call the phylogenetic school "has nothing to do with phylogeny, and is in fact what Old World biologists call the 'typologic school.'" I conclude that the unqualified assumption of correspondence between overall similarity and recency of common ancestry is not even a valid hypothesis, and that what I call the phylogenetic school of taxonomy has too much to do with phylogeny.

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